



Diversity of *Mulgedio-Aconitetea* communities in the Sudetes Mts. (SW Poland) in the Central European context

Krzysztof Świerkosz¹, Kamila Reczyńska²

¹ Museum of Natural History, Faculty of Biological Sciences, University of Wrocław, Wrocław, Poland

² Department of Botany, Faculty of Biological Sciences, University of Wrocław, Wrocław, Poland

Corresponding author: Kamila Reczyńska (kamila.reczynska@uwr.edu.pl)

Academic editor: Jürgen Dengler ♦ Received 16 June 2021 ♦ Accepted 23 December 2021 ♦ Published 9 March 2022

Abstract

Aims: To describe the compositional and ecological diversity of *Mulgedio-Aconitetea* communities in the Sudetes Mts. and their foothills. **Study area:** The Sudetes Mts. (Southwestern Poland). **Methods:** A total of 399 vegetation relevés from own field studies and the literature were sorted into groups that match the higher syntaxa of the EuroVegChecklist and associations described in the literature. Diagnostic species of the so delimited associations were determined with the phi-coefficient of association, and maps of the associations produced. Direct ordination methods were applied to identify the main environmental gradients shaping the plant communities. **Results:** We distinguished nine associations, belonging to four alliances: submontane and colline communities (*Petasition officinalis*: *Geranio phaei-Urticetum dioicae*, *Petasitetum hybridum*, *Chaerophyllo hirsuti-Petasitetum albi*, *Prenanthesetum purpureae*), upper montane nitrophilous communities (*Rumicion alpini*: *Rumicetum alpini*); subalpine communities with a dominance of graminoids and ferns (*Calamagrostion villosae*: *Poo chaixii-Deschampsietum cespitosae*, *Crepido conyzifoliae-Calamagrostietum villosae*, *Athyrietum filicis-feminae*) and subalpine tall-herb communities (*Adenostylion alliariae*: *Cicerbitetum alpinae*). Altitude, light availability, and bedrock type, which determines nutrient availability and soil reaction, played an important role in differentiating the studied communities. **Conclusions:** For convenience, we placed the four alliances in four separate orders as in the EuroVegChecklist. The fact that our ordination diagram separated only two main groups suggests the need of further research in this matter.

Taxonomic reference: Euro+Med (2006-) for vascular plants.

Syntaxonomic reference: Higher syntaxa follow Mucina et al. (2016).

Abbreviations: db-RDA = distance-based redundancy analysis; EIV = Ellenberg indicator value; pANOVA = permutational analysis of variance; PCoA = principal coordinates analysis.

Keywords

Adenostylion alliariae, *Calamagrostion villosae*, Central Europe, hygrophilous species, montane vegetation, *Mulgedio-Aconitetea*, *Petasition officinalis*, Poland, *Rumicion alpini*, synecology, syntaxonomy, tall-herb community

Introduction

Montane to subalpine tall-herb communities of Europe, Siberia and Greenland are classified in the class *Mulgedio-Aconitetea* Hadač et Klika in Klika et Hadač

1944. They include communities of tall forbs, ferns and graminoids found close to high altitude watercourses or growing within the vast areas of subalpine grasslands. According to the most comprehensive syntaxonomic overview to date, the class encompasses tall-herb communities

of eutrophic habitats on raw alluvia of streams in the upper colline to supramontane belts (Mucina et al. 2016). Due to the mosaic character of montane vegetation, which is often due to microhabitats created by glacial relief or intense erosion, communities of different phytosociological classes may co-occur with each other even at small spatial scales. Therefore, the classification of tall-herb communities is extremely complicated, as reflected by different systems throughout Central European countries that are usually incompatible with one another. For instance, in Poland, 15 associations and two alliances are distinguished within the class *Mulgedio-Aconitetea* (Matuszkiewicz 2012), in Czechia 13–16 associations and five alliances (Kočí 2001, 2007; Kočí et al. 2003), in Slovakia 32 associations within eight alliances (Kliment et al. 2004; Jarolímek et al. 2008; Šibíková et al. 2008) and in Austria (excluding the *Alnion viridis* Schnyder 1930) 12 associations and four alliances (Karner and Mucina 1993). An ambitious attempt to organize these jigsaw puzzles down to the level of alliances and associations across Central and Northern Europe was undertaken by Michl et al. (2010). A noticeable consequence of the study by Michl et al. (2010) was a significant reduction in the number of associations described from individual mountain ranges and their inclusion in syntaxa with broader distribution. From Western and Central Europe (including the Pyrenees, Massif Central, Alps, Central European highlands and Carpathians) only 19 associations within five alliances were distinguished. Later, Mucina et al. (2016) proposed a system for the higher syntaxa (alliances to class) for the whole of Europe.

The discrepancy between the systems covering Europe or larger parts thereof and local classifications of tall-herb communities in individual countries prompted us to analyze the variability of this type of vegetation in the Sudetes and their foothills. In Poland, montane tall-herb communities are still classified within the class *Betulo-Adenostyletea* Br.-Bl. 1948 and the order *Calamagrostietalia villosae* Pawłowski et al. 1928, which includes two alliances (Matuszkiewicz 2012; cited names and authorities according to this source without check). In the first alliance, *Adenostylion alliariae* Br.-Bl. 1926, there are nine associations, of which seven have been reported from the Sudetes Mts. (Matuszkiewicz 2012): *Aconitum firmit* Pawłowski, Sokołowski et Wallich 1927, *Adenostyletum alliariae* Pawłowski, Sokołowski et Wallich 1928, *Petasitetum albi* Zlatník 1928, *Salicetum lapponum* Zlatník 1928, *Athyrietum distentifolii* Hadač 1955 em. W. Matuszkiewicz 1960, *Arunco-Doronicetum austriaci* Kornaś in Kornaś et Medwecka-Kornaś 1967 and *Pado borealis-Sorbetum aucupariae* Matuszkiewicz and Matuszkiewicz 1974 (compare Zlatník 1928; Macko 1950; Matuszkiewicz and Matuszkiewicz 1974). Within the second alliance, *Calamagrostion* Luquet 1926, there are six associations, including two occurring in the Polish part of the Sudetes Mts. (Matuszkiewicz 2012): *Crepidum conyzifoliae-Calamagrostietum villosae* (Zlatník 1925) Jeník 1961 and *Bupleuro-Calamagrostietum arundinaceae* (Zlatník 1928) Jeník 1961 (comp. Matuszkiewicz and Matusz-

kiewicz 1974; Kočí 2007). Polish submontane tall-herb communities are classified as the association *Phalarido-Petasitetum hybridi* Schwickerath 1933 within the *Aegopodion podagrariae* R. Tx. 1967 alliance of the class *Artemisietea vulgaris* Lohmayer, Passarge et R. Tx. in R. Tx. 1950 (Matuszkiewicz 2012).

Besides the above-mentioned associations, from the Polish side of the Sudetes Mts. and their foothills the following association-level syntaxa were reported: *Geranio phaei-Urticetum* Hadač et al. 1969 (Świerkosz et al. 2002; Świerkosz and Reczyńska 2013), *Prenanthes purpureae* Bolleter 1921 (Świerkosz and Reczyńska 2013, 2016), *Viola sudeticae-Deschampsietum cespitosae* (Jeník et al. 1980) Kočí 2001 (Świerkosz and Reczyńska 2016), comm. *Petasites hybridus-Primula elatior* and comm. *Polygonatum verticillatum-Ranunculus platanifolius* (Świerkosz and Reczyńska 2016). The occurrence of the association *Petasitetum kablikiani* Walas 1933 in the only relict locality in the Karkonosze Mts. (Mały Śnieżny Kocioł Cirque) was reported by Uziębło (2004). In total, in the Sudetes Mts. and their foothills, 16 syntaxa at the association level have been distinguished so far within the *Mulgedio-Aconitetea*.

The aims of this study are thus: i) to conduct a comprehensive analysis of diversity of tall-herb communities of the *Mulgedio-Aconitetea* in the Sudetes Mts., assign the terminal units to described associations and place them into the higher syntaxa of the EuroVegChecklist (<https://www.synbiosys.alterra.nl/evc/>; Mucina et al. 2016); ii) to determine diagnostic species of these communities in the regional context; and iii) to identify the ecological factors influencing community species composition.

Study area

Our research was conducted on the whole area of the Sudetes, a mountain range in southwestern Poland extending over a length of 300 km and covering together with its foothills approximately 5,550 km² (Figure 1). The altitude extends across 1400 m (the highest peak is Śnieżka Mt., 1602 m a.s.l.), which is sufficient for the formation of diverse vegetation belts, from the foothills to the subalpine zone, marked by typical communities. In turn, the longitudinal location of the range causes suboceanic species to occur in the western part (e.g., *Meum athamanticum*, *Chrysosplenium oppositifolium*), while in the eastern part, Carpathian and Alpine elements occur (e.g., *Sesleria sadlerana* subsp. *tatrae*, *Scabiosa lucida*, *Cardamine trifolia*). The geological structure of the Sudetes Mts. is complex. Acidic rocks, both plutonic (granites) and sedimentary (gneisses, shales, sandstones), predominate here, but there are numerous intrusions of nutrient-rich, effusive rocks (basalts, trachytes, andesites) and metamorphic rocks (greenstones and greenschists, marbles, crystal limestones and dolomites). Thus, different types of soils derive from the diverse bedrocks – from initial soils and podzols, which are extremely poor in nutrients, through brown soils, to nutrient-rich calcareous

rendzinas (Blachowski et al. 2005). The average annual temperature ranges from 8.9°C in the foothills to 0.7°C on the top of Śnieżka Mt., and the precipitation reaches from 600 to 1200 mm/year. The relief is also notably diverse, with deep gorges next to vast plateaus and cones of volcanic origin. The hydrological network is well developed, with several major rivers (Nysa Łużycka, Kwis, Bóbr, Kaczawa, Bystrzyca and Nysa Kłodzka), all belonging to the Odra basin. The valleys of larger rivers are usually wide and flat, and the rivers in such sections are often partially regulated. The ravines of both larger rivers and streams are often marked by a natural hydrological regime. Due to the diversity of habitats, plant communities with vastly different ecological requirements can develop here in close proximity to each other. This also applies to tall-herb communities.

Methods

Field sampling and literature data

Between 1991 and 2020, we sampled 212 vegetation plots of the class in the Sudetes Mts. and their foothills (coordinates 15.32°E–17.23°E and 50.20°N–51.25°N), at elevations from 240 to 1400 m a.s.l. The plots were located in the terraces or banks of the stream valleys as well as within mires with tall-herbs. We chose stands that con-

tained diagnostic species for the class *Mulgedio-Aconitetea* and its subordinate syntaxa as known from the literature (Suppl. material 1). In accordance with Michl et al. (2010) and Mucina et al. (2016), we excluded vegetation plots with a shrub cover of more than 30%. According to Mucina et al. (2016) and following Kliment et al. (2010), we also considered the order *Petasito-Chaerophylletalia* Morariu 1967 ex Kopecký 1969 as belonging to the class *Mulgedio-Aconitetea*. The phytosociological material was collected using the Braun-Blanquet approach (Mueller-Dombois and Ellenberg 2002). The plot size varied from 5 m² to 60 m² (mean 21.5 m²). All the relevés were stored in a TURBOVEG database (Hennekens and Schaminée 2001).

Additionally, we used all the available relevés from the literature (Matuszkiewicz and Matuszkiewicz 1974 – 126 relevés; Uziębło 2010 – 4 relevés; Pender 1975, 1990, 1996 – 14 relevés in total; Anioł-Kwiatkowska and Malicki 2005 – 11 relevés; Berdowski and Kwiatkowski 1996 – 4 relevés) and unpublished data from the Polish Vegetation Database (Kącki and Śliwiński 2012 – 28 relevés) resulting in 187 additional relevés. In total, we thus used 399 relevés.

The relevés are available *via* the Polish Vegetation Database (Global Index of Vegetation-Plot Databases, ID: EU-PL-001; Kącki and Śliwiński 2012). Additionally, our own original relevés are available upon request through the VESTA Database (ID: EU-PL-004 in the Global Index of Vegetation-Plot Databases).

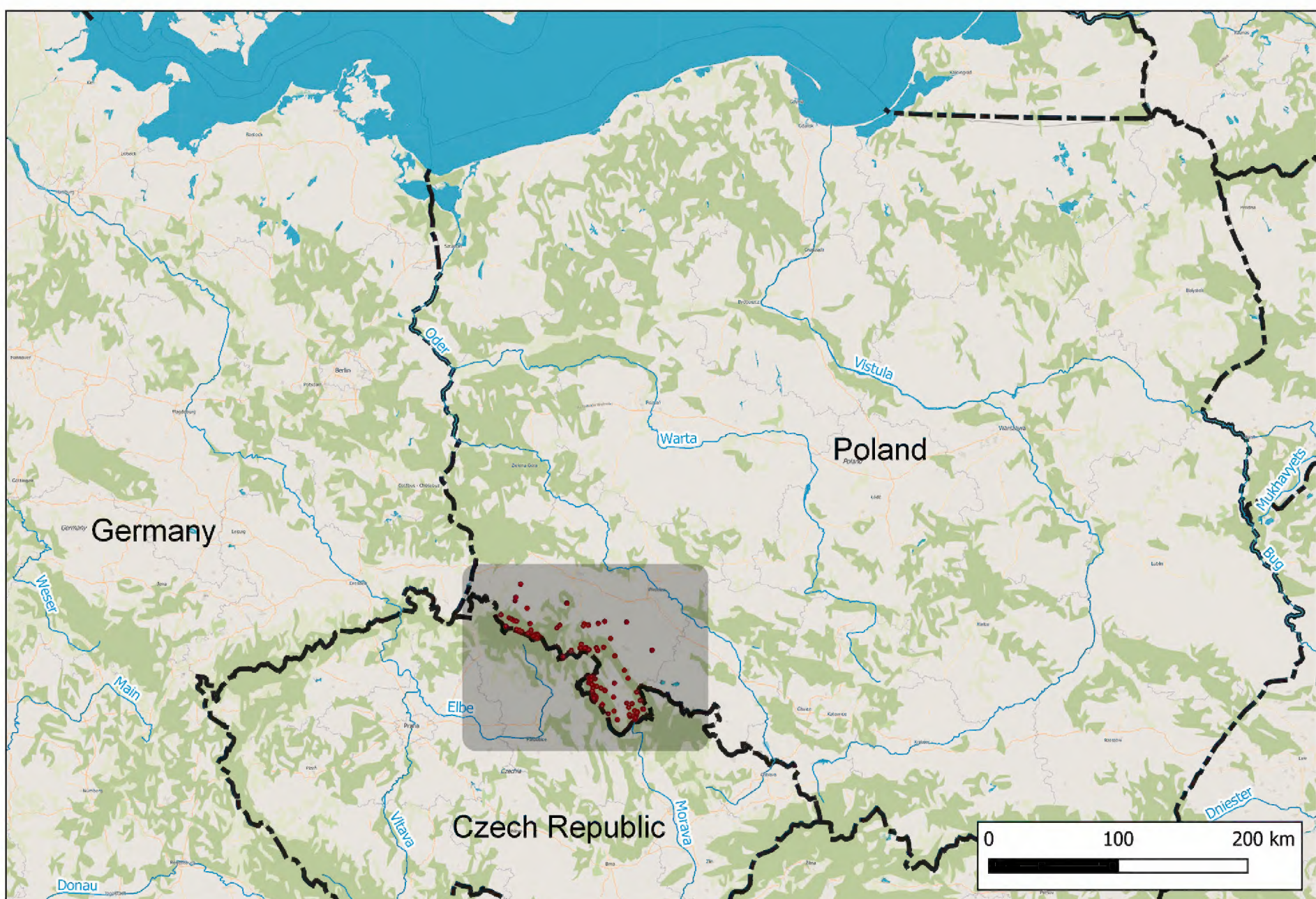


Figure 1. Area of the investigation. Red dots show the distribution of the analyzed relevés of tall-herb communities ($n = 399$) in SW Poland (gray rectangle). Forests are marked in green. Background from © MapTiler © OpenStreetMap contributors.

Environmental variables

In order to identify the ecological conditions of the tall-herb communities within the study area, different environmental variables were analyzed. Elevation (measured in m a.s.l. and divided by 1000 for presentation), slope, heat load and bedrock type were used as explanatory variables. The bedrock type at each site was obtained from the Detailed Geological Map of the Sudetes Mts. (Polish Geological Institute, National Research Institute, <http://sudety.pgi.gov.pl>). Based on the criterion of mineral composition and major geological processes (Bolewski and Parachoniak 1988), six main categories of rocks were considered as explanatory variables: Quaternary Pleistocene deposits (postglacial sands, clays and gravels), Quaternary Holocene deposits in the stream valleys, metamorphic rocks (gneisses, schists), plutonic (granitoids), acidic sedimentary (sandstones) and calcicolous rocks (limestone mudstones and marbles). According to McCune and Keon (2002) the heat load was used instead of aspect because aspect is a “circular” variable with $0^\circ = 360^\circ$. As there were no direct measurements of light and soil conditions, we used Ellenberg indicator values (EIVs) (Ellenberg et al. 1991), corrected by datasets of Berg et al. (2017) with reference to values of continentality. EIVs weighted by percentage species’ cover were calculated for each relevé using the JUICE software (Tichý and Holt 2006).

Phytosociological analysis

Prior to the analyses, occurrences of the same species in different vertical layers were merged using the procedure implemented in JUICE, under the assumption that the overlap of layers is random (Fischer 2015). Bryophytes were excluded from the analysis as they had been recorded only in part of the plots.

We conducted an unsupervised classification with the modified TWINSpan algorithm (Roleček et al. 2009) with total inertia measure of heterogeneity as implemented in JUICE software (Tichý 2002). Based on the expert evaluation of the initial clusters, we merged and re-arranged some of them (Suppl. material 2). Diagnostic species of the so derived terminal clusters (associations) were then determined using the Φ coefficient as a measure of fidelity for clusters of equalized size (Chytrý et al. 2002; Tichý and Chytrý 2006; Willner et al. 2009). Species with $\Phi \geq 0.25$, constancy $\geq 20\%$, constancy ratio (Dengler et al. 2005) ≥ 1.3 and statistically significant concentration in a particular cluster, tested by the Fisher’s exact test ($p < 0.05$), were considered diagnostic. A species was considered diagnostic for more than one cluster with $\Phi > 0.25$ in at least two clusters and a constancy ratio of ≥ 1.3 . Species with constancy ratio < 1.3 and/or $\Phi > 0.25$ in one or more clusters were not considered diagnostic but are also presented in Table 1. Constant species were defined as species with frequency of at least 50% in a particular cluster and dominant species as those with cover

$> 75\%$ (5 on a Braun-Blanquet’s cover scale) at least in a single relevé in this cluster. Based on literature sources (Kočí 2007; Stachurska-Swakoń 2009; Michl et al. 2010; Kliment et al. 2010) we classified the diagnostic species as either regional character or differential species. Then, we produced distribution maps of the syntaxa using QGIS 3.16 (with support of © MapTiler © OpenStreetMap contributors). For the associations, we used names according to the Michl et al. (2010) and Kliment et al. (2010) without checking in detail their validity according to the ICPN (Theurillat et al. 2021). Finally, the associations were arranged into the higher syntaxa of the EuroVegC-checklist (<https://www.synbiosys.alterra.nl/evc/>; Mucina et al. 2016) by expert judgement.

Ecological analysis

A principal coordinates analysis (PCoA) was performed in CANOCO (Ter Braak and Smilauer 2012) both to explore differentiation of recognized groups and to check the percentage of variation explained. Species percentage cover data were transformed with $\log(x + 1)$, and the distance matrix (399×399) was calculated using the percentage difference (SQRT Jaccard binary distance). The distribution of the sample groups was visualized with a PCoA diagram. To identify the statistical significance of correlations (using Spearman’s coefficient) between the PCoA sample scores obtained from CANOCO and mean randomized EIVs for relevés, a modified permutation test with 499 unrestricted permutations was conducted. The test was performed with MoPeT_v1.2.r script (Zelený and Schaffers 2012) in the R software (R Development Core Team 2021). Permutational analysis of variance (one-way pANOVA on the mean randomized EIVs) and modified permutation test (with 499 unrestricted permutations) were also calculated using MoPeT_v1.2.r (Zelený and Schaffers 2012), to determine which EIVs differentiate the selected communities. Using pANOVA is as an alternative to other tests under non-normal conditions, because it does not operate under the assumption of normality and uses actual scores (Gleason 2013).

To identify the main ecological drivers affecting the diversity of distinct groups, a distance-based redundancy analysis (db-RDA), embedded in CANOCO 5.0 (Ter Braak and Smilauer 2012) with SQRT Jaccard binary distance, and the variation was explained (Jupke and Schäfer 2020). A standard Monte Carlo permutation test with 499 unrestricted permutations under the full model was conducted to identify the significance of the simple term and conditional effects of environmental variables (elevation, slope, heat load and the main bedrock type) on the species composition of the analyzed samples (Ter Braak and Smilauer 2012). The conditional effect expresses the variation explained by a single explanatory variable, whereas the others are used as covariables. The simple effect expresses the variation explained by the single explanatory variable without covariables.

Results

In the analyzed data we could distinguish nine groups of tall-herb communities (Table 1, Figure 2, Suppl. material 3). We interpreted the nine groups as associations described in the literature and placed them in the higher hierarchies of the EuroVegChecklist as follows:

Proposed syntaxonomic scheme

Cl. *Mulgedio-Aconitetea* Hadač et Klika in Klika et Hadač 1944

O. *Petasito-Chaerophylletalia* Morariu 1967 ex Kopecký

All. *Petasion officinalis* Sillinger 1933

Group 1: *Geranio phaei-Urticetum dioicae* Hadač et al. 1969

Group 2: *Petasitetum hybridi* Imchenetzky 1926

Group 3: *Chaerophyllo hirsuti-Petasitetum albi* Sýkora et Hadač 1984

Group 4: *Prenanthesetum purpureae* Bolleter 1921

O. *Senecioni rupestris-Rumicetalia alpini* Mucina et Karner 2016

All. *Rumicion alpini* Scharfetter 1938

Group 5: *Rumicetum alpini* Beger 1922

O. *Calamagrostietalia villosae* Pawłowski et al. 1928

All. *Calamagrostion villosae* Pawłowski et al. 1928

Group 6: *Poo chaixii-Deschampsietum cespitosae* Pawłowski et Walas 1949

Group 7: *Crepido conyzifoliae-Calamagrostietum villosae* (Zlatník 1925) Jeník 1961

Group 8: *Athyrietum filicis-feminae* Wendelberger in Höfler et Wendelberger 1960

O. *Adenostyletalia alliariae* Br.-Bl. 1930

All. *Adenostylion alliariae* Br.-Bl. 1926

Group 9: *Cicerbitetum alpinae* Bolleter 1921

The nine associations clearly differ in terms of diagnostic species (Table 1, Suppl. material 3). Moreover, they show distinct distribution (Figure 2), physiognomy (Figures 3–5), species composition (Figure 6) as well as main ecological indicators (Table 2, Table 3, Figure 7).

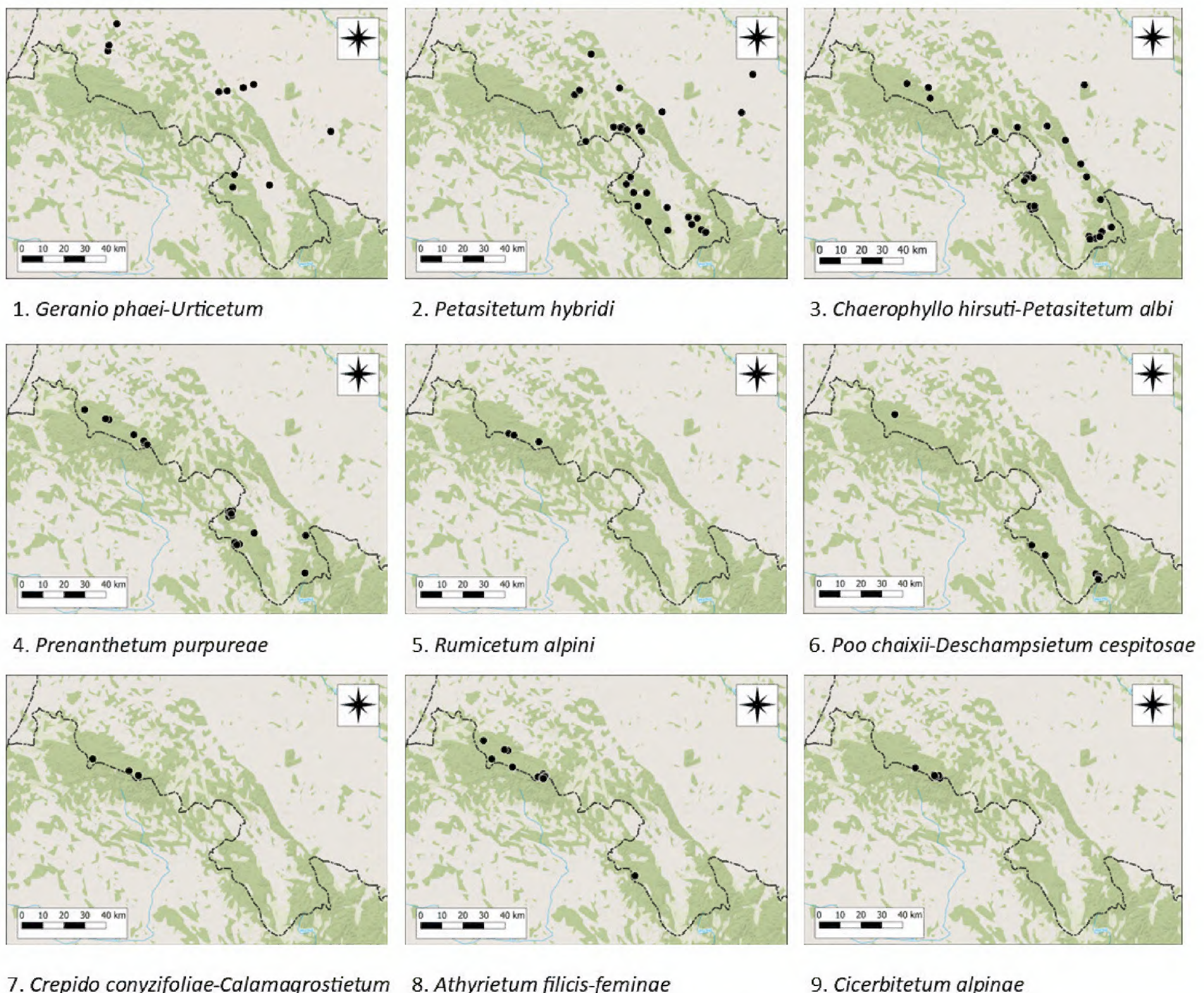


Figure 2. Distribution maps of the distinguished associations of tall-herb communities of the Sudetes Mts. and their foothills. The numbers refer to the group IDs used throughout this paper. Background from © MapTiler © OpenStreetMap contributors.

Description of distinguished groups of relevés

In the following, among the diagnostic species, the character species (in bold) are highlighted (see Table 1).

Group 1 – *Geranio phaei-Urticetum dioicae* Hadač et al. 1969

Number of relevés: 33

Diagnostic species: *Geranium phaeum*, *Alliaria petiolata*, *Chaerophyllum aromaticum*, *Ch. temulum*, *Geum urbanum*, *Glechoma hederacea*, *Poa nemoralis*, *Schedonorus giganteus*, *Stellaria holostea*, *Ulmus glabra*, *Aegopodium podagraria*, *Galium aparine*, *Mercurialis perennis*

Constant species: *Aegopodium podagraria*, *Chaerophyllum aromaticum*, *Geranium phaeum*, *Geum urbanum*, *Urtica dioica*

Dominant species: *Geranium phaeum*

Ecology: The association was found at elevations between 200 and 750 m a.s.l. (mean 406 m a.s.l.), thus is submontane/montane in character. It occurred mainly on terraces of streams developing on Quaternary Pleistocene deposits, only exceptionally on Holocene sands and gravels. It usually accompanies nitrophilous alluvial forest communities of the *Carpino-Fagetea* Jakucs ex Passarge 1968 class, for example, in gaps of the stand or in places devoid of trees and shrubs.

Group 2 – *Petasitetum hybridi* Imchenetzky 1926

Number of relevés: 59

Diagnostic species: *Petasites hybridus*, *Phalaroides arundinacea*, *Anthriscus sylvestris*, *Filipendula ulmaria*, *Cirsium oleraceum*, *Aegopodium podagraria*, *Galium aparine*, *Poa trivialis*, *Rumex acetosa*

Constant species: *Aegopodium podagraria*, *Cirsium oleraceum*, *Petasites hybridus*, *Urtica dioica*

Dominant species: *Petasites hybridus*

Ecology: The association was found at elevations between 300 and 964 m a.s.l. (mean 532 m a.s.l.), indicating its submountain and lower-mountain character. It was recorded mainly in stream valleys over Quaternary Holocene deposits, and only exceptionally over postglacial formations. Most of the documented stands occurred in the vicinity of submontane riparian forests, but in large, open and sunny clearings. The succession of trees and shrubs in such tall-forb patches is low, which may indicate regular floods of watercourses, increasing the mortality rate of seedlings of woody forms.

Group 3 – *Chaerophyllo hirsuti-Petasitetum albi* Sýkora et Hadač 1984

Number of relevés: 74

Diagnostic species: *Petasites albus*, *Carex sylvatica*, *Fraxinus excelsior*, *Impatiens noli-tangere*, *Lysimachia nemorum*, *Ajuga reptans*, *Athyrium filix-femina*, *Senecio ovatus*, *Stachys sylvatica*

Constant species: *Athyrium filix-femina*, *Chaerophyllum hirsutum*, *Lamium galeobdolon* agg., *Oxalis acetosella*, *Petasites albus*, *Senecio ovatus*, *Stellaria nemorum*, *Urtica dioica*

Dominant species: *Petasites albus*

Ecology: The association was found at elevations of 375–995 m a.s.l. (mean 695 m a.s.l.), indicating its submontane/lower-montane character. It usually accompanies nitrophilous, deciduous forest communities of the *Carpino-Fagetea* class – mainly alluvial forests, but also nitrophilous beech or ravine woods. This association was recorded from all types of analyzed bedrock, most often on Holocene gravels in stream valleys, but also on sedimentary and metamorphic rocks. Therefore, it does not appear to show any preferences regarding bedrock type and is one of the most widely distributed communities within the alliance. Stands over calcareous rocks are richer in species, with the inclusion of *Delphinium elatum*, *Ranunculus platanifolius* or *Aconitum variegatum*, and resemble the *Delphinietum elatae* Beger ex Sutter 1978. However, so far only one locality of that type is known in the Kleśnica Valley (Eastern Sudetes, Śnieżnik Massif, about 800 m a.s.l.).

Group 4 – *Prenanthes purpureae* Bolleter 1921

Number of relevés: 51

Diagnostic species: *Prenanthes purpurea*, *Equisetum sylvaticum*, *Dryopteris carthusiana*, *Dryopteris dilatata*, *Gymnocarpium dryopteris*, *Fagus sylvatica*, *Phegopteris connectilis*, *Sorbus aucuparia* subsp. *aucuparia*, *Athyrium filix-femina*, *Lactuca alpina*, *Oxalis acetosella*, *Senecio ovatus*

Constant species: *Athyrium filix-femina*, *Calamagrostis villosa*, *Chaerophyllum hirsutum*, *Lactuca alpina*, *Dryopteris carthusiana*, *Lamium galeobdolon* agg., *Oxalis acetosella*, *Petasites albus*, *Senecio ovatus*, *Stellaria nemorum*

Dominant species: *Lactuca alpina*

Ecology: The association was found at elevations of (405–) 650–925 m a.s.l. (mean 758 m a.s.l.), therefore is montane in character. However, in contrast to the previous association, it accompanies acidophilous beech forests of the *Luzulo-Fagetalia sylvaticae* Scamoni et Passarge 1959 order and spruce forest communities of natural or anthropogenic origin. Stands were mainly reported from sedimentary and metamorphic rocks, rarely from Holocene gravels or granites. The association is less frequent than the previous one and is restricted to a few mountain ranges (Śnieżnik Massif, Stołowe Mts., Orlickie Mts., Izer-skie Mts. and Karkonosze Mts.).

Group 5 – *Rumicetum alpini* Beger 1922

Number of relevés: 20

Diagnostic species: *Rumex alpinus*, *Peucedanum ostruthium*, *Ochlopoa supina*, *Agrostis capillaris*, *Deschampsia cespitosa*, *Epilobium montanum*, *Festuca rubra*, *Ranunculus acris*, *Veronica chamaedrys*

Constant species: *Agrostis capillaris*, *Deschampsia cespitosa*, *Ranunculus repens*, *Rumex alpinus*, *R. arifolius*, *Senecio nemorensis*, *Stellaria nemorum*, *Urtica dioica*

Dominant species: *Rumex alpinus*

Ecology: The association was recorded at elevations of (840–) 1055–1190 m a.s.l. (mean 1063 m a.s.l.) within the lower alpine zone. It is connected to intensive human

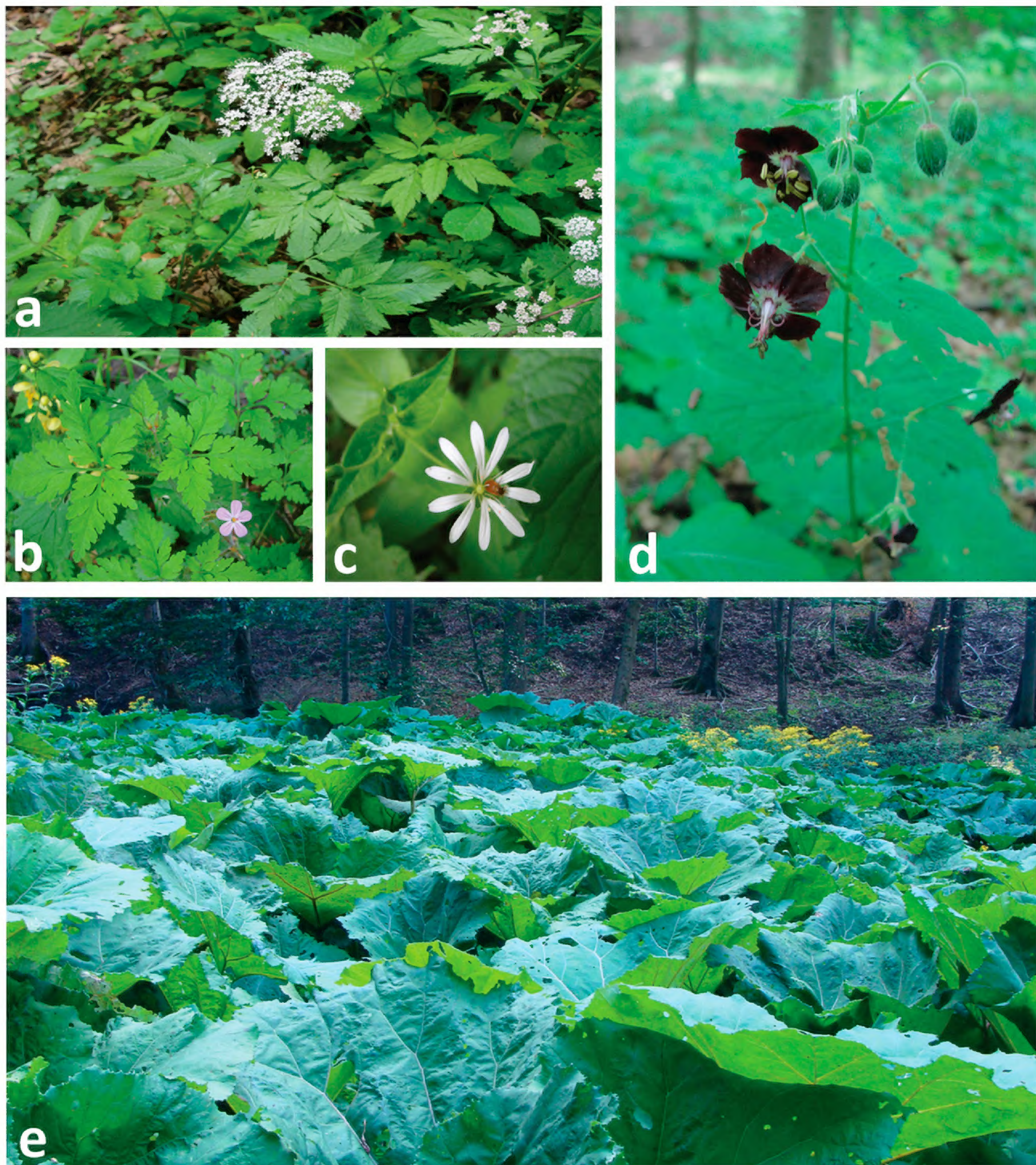


Figure 3. Tall-forb vegetation belonging to the *Petasito-Chaerophylletalia*. **a–d.** *Geranio phaei-Urticetum dioicae* components in colline location (330–380 m a.s.l. in the Pełcznica river's ravine (Wałbrzyskie Foothills, Central Sudetes) (**a.** *Chaerophyllum hirsutum*; **b.** *Geranium robertianum*; **c.** *Stellaria nemorum*; **d.** *Geranium phaeum*); **e.** *Petasitetum hybridum* in the valley of the Bystrzyca Dusznicka river, 725 m a.s.l. (Bystrzyckie Mts., Central Sudetes). (Photographs **a–d.** K. Reczyńska; **e.** K. Świerkosz).

presence, for example near montane hostels and abandoned pastures. It was found mainly on granite (Karkonosze Mts.).

Group 6 – *Poa chaixii-Deschampsietum cespitosae*
Pawłowski et Walas 1949

Number of relevés: 12

Diagnostic species: *Viola lutea* subsp. *sudetica*, *Poa chaixii*, *Cardamine opizii*, *Juncus effusus*, *Stellaria alsine*,

Viola palustris, *Agrostis canina*, *Deschampsia cespitosa*, *Oxalis acetosella*, *Stellaria nemorum*

Constant species: *Chaerophyllum hirsutum*, *Deschampsia cespitosa*, *Juncus effusus*, *Myosotis scorpioides* agg., *Oxalis acetosella*, *Ranunculus repens*, *Rumex arifolius*, *Stellaria nemorum*

Dominant species: *Deschampsia cespitosa*, *Doronicum austriacum*

Ecology: The association was found at elevations of (650–) 885–1231 m a.s.l. (mean 1024 m a.s.l.), i.e., in the

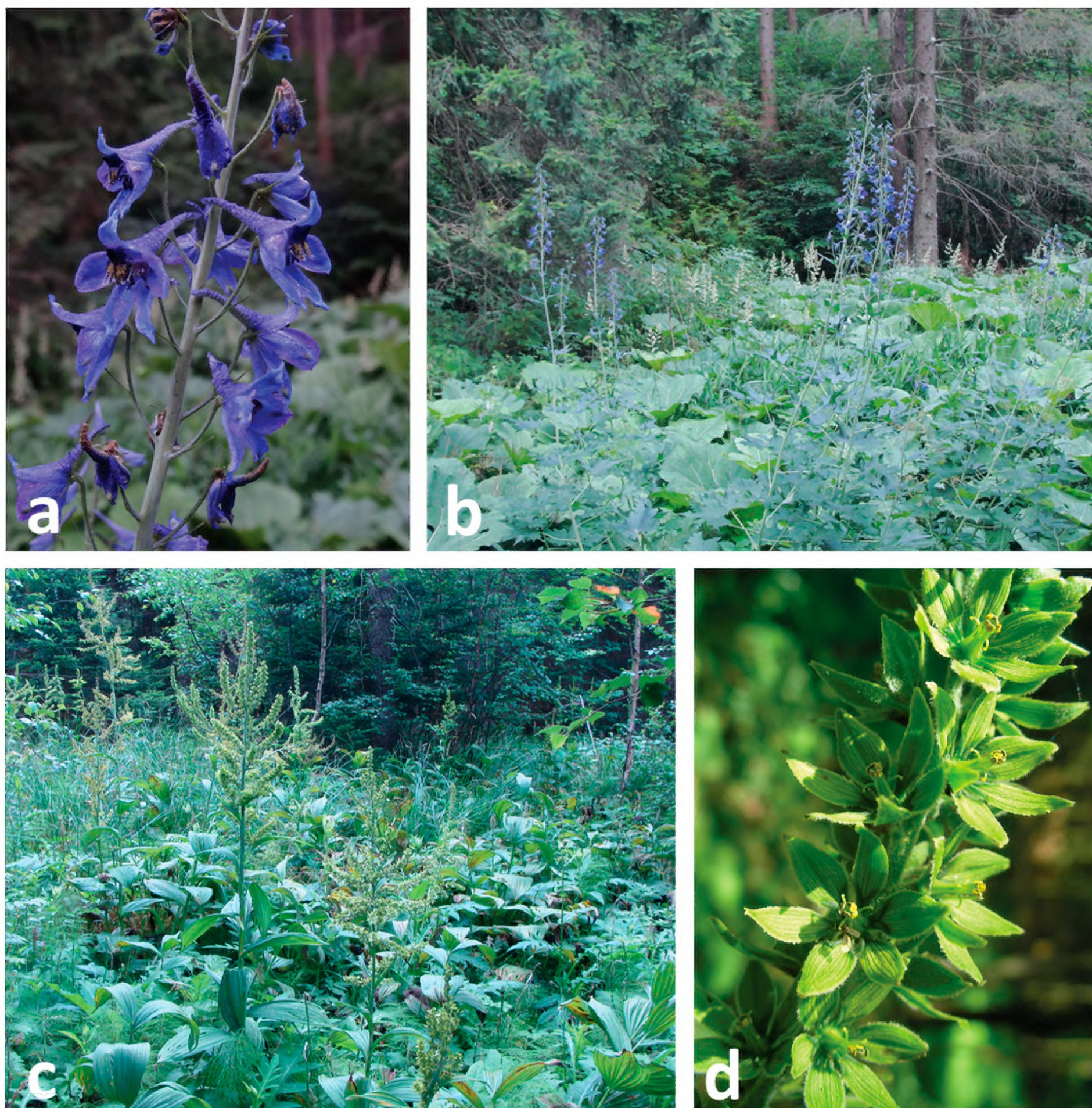


Figure 4. Tall-forb vegetation belonging to the *Petasito-Chaerophylletalia*. **a–b.** *Delphinium elatum* in the Kleśnica valley (Śnieżnik Massif, Eastern Sudetes) where it occurs in the plots of the *Petasitetum hybridi* and *Chaerophyllo hirsuti-Petasitetum albi*; **c–d.** *Prenanthes purpurea* in the Stołowe Mts. (Eastern Sudetes) with the presence of *Veratrum lobelianum*. (Photographs **a–d** K. Świerkosz).

montane and subalpine zones. In the Sudetes Mts. it was reported from the Śnieżnik Massif, Izerskie Mts., Bystrzyckie and Orlickie Mts. mainly on metamorphic rocks (schists) and, rarely, Holocene deposits.

Group 7 – *Crepido conyzifoliae*-*Calamagrostietum villosae* (Zlatník 1925) Jeník 1961

Number of relevés 61

Diagnostic species: *Anemonastrum narcissiflorum*, *Potentilla aurea*, *Pulsatilla alpina*, *Thesium alpinum*, *Achillea millefolium*, *Anthoxanthum odoratum*, *Calluna vulgaris*, *Maianthemum bifolium*, *Melampyrum sylvaticum*,

Vaccinium vitis-idaea, *Athyrium distentifolium*, *Calamagrostis arundinacea*, *Avenella flexuosa*, *Bistorta officinalis*, *Gentiana asclepiadea*, *Homogyne alpina*, *Luzula luzuloides*, *Nardus stricta*, *Polygonatum verticillatum*, *Ranunculus platanifolius*, *Silene vulgaris*, *Solidago virgaurea*, *Trientalis europaea*, *Veratrum album*

Constant species: *Anthoxanthum odoratum*, *Athyrium distentifolium*, *Bistorta officinalis*, *Calamagrostis villosa*, *Calluna vulgaris*, *Avenella flexuosa*, *Gentiana asclepiadea*, *Homogyne alpina*, *Luzula luzuloides*, *Potentilla aurea*, *Pulsatilla alpina*, *Ranunculus platanifolius*, *Rumex arifolius*, *Senecio nemorensis*, *Silene vulgaris*, *Solidago virgaurea*, *Trientalis europaea*, *Vaccinium myrtillus*, *Veratrum album*

Dominant species: *Calamagrostis villosa*

Ecology: The association was found in the Karkonosze Mts. at elevations from 1150 to 1470 m a.s.l. (mean 1287 m a.s.l.) and is subalpine in character.

Group 8 – *Athyrietum filicis-feminae* Wendelberger in Höfler et Wendelberger 1960

Number of relevés: 59

Diagnostic species: *Athyrium distentifolium*, *Lactuca alpina*, *Avenella flexuosa*, *Gentiana asclepiadea*, *Oxalis acetosella*, *Silene dioica*, *Veratrum album*

Constant species: *Athyrium distentifolium*, *Calamagrostis villosa*, *Lactuca alpina*, *Avenella flexuosa*, *Gentiana asclepiadea*, *Oxalis acetosella*, *Bistorta officinalis*, *Rubus idaeus*, *Rumex arifolius*, *Senecio nemorensis*, *Vaccinium myrtillus*, *Veratrum album*

Dominant species: *Athyrium distentifolium*

Ecology: The association was found at elevations from 770 to 1380 m a.s.l. (mean 1168 m a.s.l.), in the upper montane and subalpine zones. In the Sudetes Mts. it is reported from the Karkonosze Mts. on granites, mainly on steep slopes of the postglacial circles, and from the Orlickie and Izerskie Mts. on metamorphic bedrocks.



Figure 5. Communities of *Mulgedio-Aconitetea* in the Karkonosze Mts. and Orlickie Mts. **a.** *Aconitum variegatum* in the *Athyrietum filicis-feminae* in the Orlickie Mts. near Zieleniec; **b.** *Rumicetum alpini* in the vicinity of Hala Szrenicka montane hostel (1100 m a.s.l.) **c–d.** Subendemic *Aconitum plicatum* in the *Crepido-Calamagrostietum* (**c**) and the *Cicerbitetum alpinae* (**d**) – one of the most spectacular species occurring in subalpine tall-herb communities (1170–1260 m a.s.l.). (Photographs **b, d.** K. Reczyńska; **a, c.** K. Świerkosz).

Group 9 – *Cicerbitetum alpinae* Bolleter 1921
Number of relevés 30

Diagnostic species: *Carduus personata*, *Epilobium alpestre*, *Hieracium prenanthoides*, *Thalictrum aquilegiifolium*, *Angelica sylvestris*, *Daphne mezereum*, *Dryopteris filix-mas*, *Epilobium angustifolium*, *Heracleum sphondylium* subsp. *sphondylium*, *Milium effusum*, *Aconitum plicatum*, *Adenostyles alliariae*, *Alchemilla glabra*, *Anthriscus nitida*, *Athyrium distentifolium*, *Bistorta officinalis*, *Lactuca alpina*, *Geranium sylvaticum*, *Lilium martagon*, *Phyteuma spicatum*, *Ranunculus platanifolius*, *Silene dioica*, *Salix silesiaca*, *Veratrum album*, *Viola biflora*

Constant species: *Aconitum plicatum*, *Adenostyles alliariae*, *Alchemilla glabra*, *Athyrium distentifolium*, *Chaerophyllum hirsutum*, *Lactuca alpina*, *Deschampsia cespitosa*, *Epilobium alpestre*, *Geranium sylvaticum*, *Heracleum sphondylium* subsp. *sphondylium*, *Myosotis scorpioides* agg., *Bistorta officinalis*, *Ranunculus platanifolius*, *Rubus idaeus*, *Rumex arifolius*, *Senecio nemorensis*, *Silene dioica*, *Stellaria nemorum*, *Thalictrum aquilegiifolium*, *Valeriana excelsa* subsp. *sambucifolia*, *Veratrum album*

Dominant species: *Adenostyles alliariae*, *Lactuca alpina*
Ecology: The association was found at elevations from 1100 to 1400 m a.s.l. (mean 1277 m a.s.l.), in the upper montane and subalpine zones. In the Sudetes Mts. it is reported only from the Karkonosze Mts. on granite.

Table 1. Summarized synoptic table with percentage frequency and fidelity values derived from 399 relevés of tall-herb associations of the *Mulgedio-Aconitetea* in the Sudetes Mts. and their foothills (SW Poland). The positive Φ coefficient values (multiplied by 100) are presented as superscripts (*: 25 to 49, **: ≥ 50). Species diagnostic for both one or several clusters ($\Phi \geq 25$ and constancy ratio ≥ 1.3) are shaded in grey. Character and differentiating species were sorted according to constancy, while the other species were sorted according to the number of occurrences in clusters or resemblance to the diagnostic species in neighboring cluster. Among accompanying species, only the most common ones, which occurred in at least seven clusters, were included in the table. Abbreviations: Ch: character species; D*: regionally differentiating species (marked in the table with asterisk). Shortened names of syntaxa: *Se.Ru.*: order *Senecioni rupestris-Rumicetalia alpini*; *Cal.vill.*: order *Calamagrostietalia villosae*; *Ad.al.*: order *Adenostyletalia alliariae*; *R.al.*: alliance *Rumicion alpini*; *Ca.vi.*: alliance *Calamagrostion villosae*; *Ad.*: alliance *Adenostylium alliariae*.

Group No.	Constancy ratio	1	2	3	4	5	6	7	8	9
No. of relevés		33	59	74	51	20	12	61	59	30
Order		Petasito-Chaerophylletalia				Se.Ru		Cal.vill.		Ad. al
Alliance		Petasition officinalis				R.al.		Ca. vi.		Ad.
Ch. and D.* Geranio phaei-Urticetum										
Geranium phaeum	14	100 **	7	1
Geum urbanum*	4.5	55 **	12	5
Chaerophyllum aromaticum*	2.5	52 **	20	5	4
Glechoma hederacea*	3.1	42 **	14
Poa nemoralis*	5.9	39 *	2	4	6	.	.	.	2	7
Schedonorus giganteus*	3.3	36 *	7	11	4	.	.	.	2	.
Alliaria petiolata*	17	30 **	2
Stellaria holostea*	17	30 **	2
Ulmus glabra*	5.0	27 *	2	5
Chaerophyllum temulum*	100	21*								
Ch. and D.* Petasitetum hybrydi										
Petasites hybridus	24	.	100 **	4
Cirsium oleraceum*	1.5	9	56 *	36	14	.	8	.	2	.
Phalaroides arundinacea	100	.	41 **
Filipendula ulmaria*	1.8	9	31 *	7	.	.	.	2	.	17
Anthriscus sylvestris*	1.9	12	24 *	1
Ch. and D.* Chaerophylo hirsuti-Petasitetum albi										
Petasites albus	5.7	3	12	99 **	69	.	8	.	8	7
Impatiens noli-tangere*	1.3	12	17	46 *	35	.	17	.	3	.
Stachys sylvatica*	1.6	27	25	45*	24
Carex sylvatica*	3.2	9	12	45 *	14
Lysimachia nemorum*	1.6	.	2	28 *	18	.	17	.	2	.
Fraxinus excelsior*	2.6	6	10	27 *	8	.	.	.	2	.
Ch and D.* Prenanthesetum purpureae										
Dryopteris carthusiana*	1.8	.	.	16	53 *	.	25	.	27	7
Equisetum sylvaticum*	1.8	.	5	24	49 *	5	42	.	.	.
Prenanthes purpurea	1.3	.	2	18	47*	.	17	11	34	17
Sorbus aucuparia subsp. aucuparia*	2.5	.	.	8	47 *	.	17	7	19	.
Dryopteris dilatata*	1.6	.	.	4	41 *	.	8	7	25	10
Gymnocarpium dryopteris*	4.0	.	.	4	33 *	.	8	.	3	7
Fagus sylvatica*	1.5	.	1	15	24 *	2
Phegopteris connectilis*	2.1	.	.	7	22 *	.	.	.	10	.
Ch. Rumicetum alpini										
Rumex alpinus	51	.	.	.	2	100**
Peucedanum ostruthium	100	35**
Ch. and D.* Poo-Deschampsietum cespitosae										
Juncus effusus *	2.9	.	3	8	6	20	58 **	.	3	.
Viola lutea subsp. sudetica	100	42 **	.	.	.
Cardamine opizii *	100	33 **	.	.	.
Poa chaixi	1.3	.	.	4		10	33 *	15		27
Viola palustris*	17	.	2	1	2	.	33 *	.	.	.



Group No.	Constancy ratio	1	2	3	4	5	6	7	8	9
No. of relevés		33	59	74	51	20	12	61	59	30
Order		Petasito-Chaerophylletalia				Se.Ru		Cal.vill.		Ad. al
Alliance		Petasition officinalis				R.al.		Ca. vi.		Ad.
<i>Stellaria alsine</i> *	6.5	.	2	3	.	.	33 *	.	5	.
Ch. and D.* <i>Crepido conyzifoliae</i>-<i>Calamagrostietum villosae</i>										
<i>Anthoxanthum odoratum</i> *	100	64 **	.	.
<i>Potentilla aurea</i>	9.7	61 **	2	7
<i>Pulsatilla alpina</i>	100	54 **	.	.
<i>Calluna vulgaris</i> *	31	54 **	2	.
<i>Melampyrum sylvaticum</i> *	22	.	.	.	2	.	.	44 **	2	.
<i>Calamagrostis arundinacea</i> *	1.3	.	.	22	12	.	17	41 *	12	30
<i>Vaccinium vitis-idaea</i> *	25	.	.	1	.	.	.	34 **	.	.
<i>Maianthemum bifolium</i> *	2.5	.	.	3	14	.	.	34 *	14	.
<i>Achillea millefolium</i> *	1.7	.	.	3	.	20	.	34 *	5	20
<i>Anemonastrum narcissiflorum</i>	100	31 **	.	.
<i>Thesium alpinum</i>	100	21 *	.	.
<i>Nardus stricta</i> *	100	21 *	.	.
Ch. and D.* <i>Cicerbitetum alpinae</i>										
<i>Thalictrum aquilegifolium</i>	4.7	.	2	11	2	.	.	15	3	70 **
<i>Heracleum sphondylium</i> *	2.3	9	24	8	2	20	.	7	2	57 *
<i>Epilobium alpestre</i>	5.3	.	.	1	.	10	.	.	.	53 **
<i>Milium effusum</i> *	3.5	3	2	4	6	15	8	.	12	53 *
<i>Epilobium angustifolium</i> *	3.6	5	.	15	5	53 *
<i>Carduus personata</i>	5.2	.	5	9	2	.	8	.	.	50 *
<i>Dryopteris filix-mas</i> *	2.1	12	.	20	18	.	8	11	19	43 *
<i>Daphne mezereum</i> *	4.7	.	2	4	.	.	8	7	3	40 *
<i>Angelica sylvestris</i> *	1.4	.	20	1	6	.	.	.	3	30 *
<i>Hieracium prenanthoides</i>	8.1	3	2	27 *
D*. All. <i>Petasition officinalis</i>										
<i>Aegopodium podagraria</i> *	1.9	85 **	68 *	35	14
<i>Galium aparine</i> *	23	39 *	32 *	1
<i>Poa trivialis</i> *	1.3	9	34 *	7	2	25	8	.	2	3
<i>Mercurialis perennis</i> *	1.4	27 *	3	19	6
<i>Lamium maculatum</i> *	1.3	18	25 *	4
<i>Ajuga reptans</i> *	3.6	6	2	22 *	6
<i>Pulmonaria obscura</i> *	2.8	6	3	17 *	4
<i>Acer pseudoplatanus</i> *	1	24	7	36 *	37	5	.	.	8	.
<i>Lamium galeobdolon</i> agg. *	1	48	8	53 *	61 *	.	17	.	2	.
D.* all. <i>Rumicion alpini</i>										
<i>Agrostis capillaris</i> *	3.9	65 **	17	5	7	3
<i>Festuca rubra</i> *	4.1	35 *	8	5	.	.
<i>Veronica chamaedrys</i> *	1.5	15	24	1	.	35 *
<i>Epilobium montanum</i> *	2	6	10	22	22	45 *	8	.	8	3
<i>Ranunculus acris</i> *	3	3	3	.	2	30 *	.	2	.	9
<i>Ochlopoa supina</i>	7.5	25 **	.	.	.	3
Ch and D* all. <i>Calamagrostion villosae</i>										
<i>Avenella flexuosa</i> *	1.7	.	.	.	4	5	17	95 **	58 *	33
<i>Calamagrostis villosa</i>	1.3	.	.	15	69	20	50	92 *	92 *	50
<i>Vaccinium myrtillus</i> *	1.6	.	.	4	20	.	33	90 **	56 *	6
<i>Gentiana asclepiadea</i>	1.4	.	.	.	4	5	.	57 *	49 *	33
<i>Trientalis europaea</i> *	1.9	8	67 *	37 *	.
<i>Luzula luzuloides</i> *	2.5	.	3	1	6	15	25	92 **	27	37
<i>Solidago virgaurea</i> *	3.4	.	.	4	10	.	8	82 **	24	7
<i>Homogyne alpina</i> *	2.7	.	.	1	18	5	8	79 **	29	.
<i>Luzula sylvatica</i>	4	.	8	2	8	.
<i>Galium saxatile</i>	11	3	3
Ch. and D* All <i>Adenostylion alliariae</i>										
<i>Lactuca alpina</i>	4.7	.	.	11	84 *	.	8	15	69 *	87 *
<i>Ranunculus platanifolius</i>	1.9	.	2	7	10	.	8	74 *	37	73 *
<i>Aconitum plicatum</i>	1.7	.	.	1	.	.	33	21	14	87 **
<i>Adenostyles alliariae</i>	1.9	.	.	1	.	20	.	26	44	87 **
<i>Viola biflora</i>	3.8	.	.	4	2	.	.	13	7	50 **
<i>Lilium martagon</i> *	1.4	3	2	3	2	.	.	30	5	43 *
<i>Geranium sylvaticum</i>	2.7	.	15	7	.	.	17	28	6	77 **
Class <i>Mulgedio-Aconitetea</i>										
<i>Senecio nemorensis</i>	19	.	2	4	2	85 *	.	79 *	78 *	100 *
<i>Athyrium distentifolium</i>	6.3	.	.	4	8	10	.	64 *	97 **	67 *
<i>Veratrum album</i>	2.2	.	3	18	31	.	8	82 *	71 *	77 *
<i>Silene dioica</i>	2.9	12	17	7	2	10	8	15	51 *	63 *
<i>Silene vulgaris</i> *	1.6	5	8	57 *	5	37 *
<i>Anthriscus nitida</i>	1.9	15	5	14	8	.	8	.	.	30 *
<i>Alchemilla glabra</i>	1.7	30	25	.	3	53 *
<i>Valeriana excelsa</i> subsp. <i>sambucifolia</i>	4.6	3	.	11	4	.	.	2	5	50 *
<i>Phyteuma spicatum</i>	2.0	9	3	11	20	5	.	25	2	50 *
<i>Salix silesiaca</i>	3.0	.	2	4	.	.	8	11	12	37 *
<i>Stellaria nemorum</i>	1.4	21	34	69	69	70	100 *	2	36	60
<i>Polygonatum verticillatum</i>	1.5	.	.	19	27	.	.	46 *	27	30
<i>Rumex arifolius</i>	1.1	.	2	9	.	65	75	75	86 *	93 *
<i>Chaerophyllum hirsutum</i>	.	21	49	77	84	50	83	.	14	77
<i>Streptopus amplexifolius</i>	.	.	.	15	33	.	8	20	24	40 *
<i>Primula elatior</i>	.	21	20	27	18	.	8	2	.	23

Group No.		1	2	3	4	5	6	7	8	9
No. of relevés	Constancy ratio	33	59	74	51	20	12	61	59	30
Order		<i>Petasito-Chaerophylletalia</i>				<i>Se.Ru</i>		<i>Cal.vill.</i>		<i>Ad. al</i>
Alliance		<i>Petasition officinalis</i>				<i>R.al.</i>		<i>Ca. vi.</i>		<i>Ad.</i>
<i>Aconitum variegatum</i>		.	2	9	4	.	17	.	2	3
<i>Delphinium elatum</i>		.	3	3	2
<i>Campanula latifolia</i>		.	2	5	2	3
Diagnostic for more than one association										
<i>Oxalis acetosella</i>	1.3	21	7	59	90 *	10	92 *	11	83 *	1
<i>Bistorta officinalis</i>	4.0	.	14	.	.	15	8	92*	61*	63*
<i>Senecio ovatus</i>	1.6	30	19	69 *	71 *	25	42	2	24	7
<i>Athyrium filix-femina</i>	1.3	6	7	72 *	69 *	5	50	.	10	.
<i>Deschampsia cespitosa</i>	1.4	9	15	9	14	85 *	92 *	48	39	60
Common accompanying species (at least in 7 groups)										
<i>Crepis paludosa</i>		3	27	41	49	15	17	3	8	33
<i>Rubus idaeus</i>		9	8	42	41	25	8	30	61	60
<i>Hypericum maculatum</i>	.		10	4	4	35	17	41	15	30
<i>Ranunculus repens</i>	1	21	36	30	29	55	58 *	.	8	3
<i>Myosotis scorpioides</i> agg.	1.2	.	17	26	27	15	67 *	5	8	53
<i>Urtica dioica</i>	1.1	91 *	78 *	65	35	70	25	.	5	20
<i>Picea abies</i>	1.1	.	3	14	35	.	42 *	3	15	7
<i>Alchemilla monticola</i> agg.		9	14	3	4	.	.	2	14	12
<i>Dactylis glomerata</i>	1.1	27	39	15	8	45 *	25	.	3	.
<i>Chrysosplenium alternifolium</i>		.	14	41	29	15	33	.	7	30

Ecological differentiation

As shown in the PCoA ordination diagram, the nine associations fall within two clusters that were clearly separated along the first PCoA axis (Figure 6). Associations 1–6 were in the cluster with low PCoA1 values, while associations 7–9 with the exception of few relevés of association 8, were in the cluster with high PCoA1 values. Within the left-hand cluster (low PCoA1 values), the associations largely overlapped, particularly association 1 and 2, as well as associations 3, 4 and 6. By contrast, the three associations of the right-hand cluster were quite well separated from each other. The first and the second PCoA axes explained 8.8% and 4.2% of compositional variability of studied communities, respectively. The first PCoA axis was significantly negatively correlated with the EIVs for soil reaction ($p < 0.05$), nutrients ($p < 0.05$) and temperature ($p < 0.01$). The second and third PCoA axes were significantly and positively correlated with the EIVs for light ($p < 0.01$) and moisture ($p < 0.05$), respectively (Table 2).

Table 2. Significance of Spearman's rank correlation of mean EIVs with three main PCoA axes within the tall-herb communities in the Sudetes Mts. and their foothills using modified permutation test.

	Axis 1		Axis 2		Axis 3	
	ρ^1	p^2	ρ	p	ρ	p
EIV temperature	-0.77**	0.004	0.32	0.220	-0.08	0.696
EIV soil reaction	-0.73*	0.012	0.34	0.164	0.32	0.108
EIV nutrients	-0.71*	0.020	0.29	0.300	0.39	0.052
EIV light	0.46	0.192	0.64**	0.008	0.33	0.056
EIV moisture	-0.48	0.164	-0.12	0.624	0.40*	0.032

¹ Spearman's ρ estimate; ² modified,* - $p < 0.05$, ** - $p < 0.01$.

The pANOVA revealed that temperature played a significant role in the floristic differentiation of the nine associations ($p < 0.05$). In contrast, the other analyzed EIVs for nutrients, soil reaction, moisture and light were not significant (Figure 7).

The db-RDA (Figure 8) revealed that the explanatory variables used in the analysis accounted for 13.5% of the total variation in species composition (while R^2_{adj}

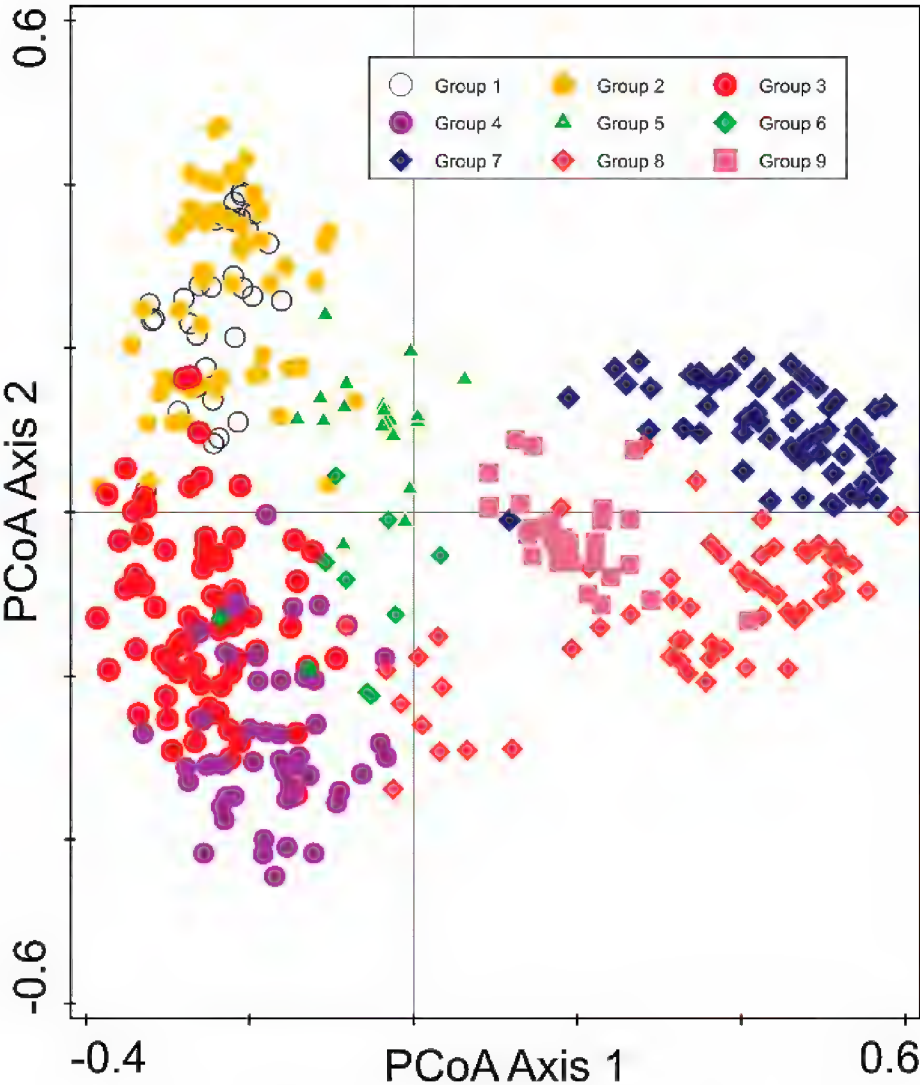


Figure 6. PCoA diagram for the 399 vegetation plots of tall-herb communities in the Sudetes Mts. and their foothills (SW Poland). The numbers of clusters are identical with Figure 2. Clusters 1 and 2 refer to submontane communities on nutrient-rich, Quaternary deposits; cluster 3 and 4 represent phytocoenoses in shaded sites, located within forest stands in the lower alpine zone; clusters 5 to 9 represent light-demanding and slightly acidophilic phytocoenoses developing from the subalpine to lower alpine zone. Symbols are grouped in alliances: circles: *Petasition officinalis*: 1 – *Geranio phaei-Urticetum*, 2 – *Petasitetum hybridi*, 3 – *Chaerophylo hirsuti-Petasitetum albi*; 4 – *Prenanthesetum purpureae*; triangles: *Rumicion alpini*: 5 – *Rumicetum alpini*; diamonds: *Calamagrostion villosae*: 6 – *Poo chaixii-Deschampsietum*, 7 – *Athyrietum filicis-feminae*, 8 – *Crepidum conyzifoliae-Calamagrostietum*; squares: *Adenostylium alliariae*: 9 – *Cicerbitetum alpinae*.

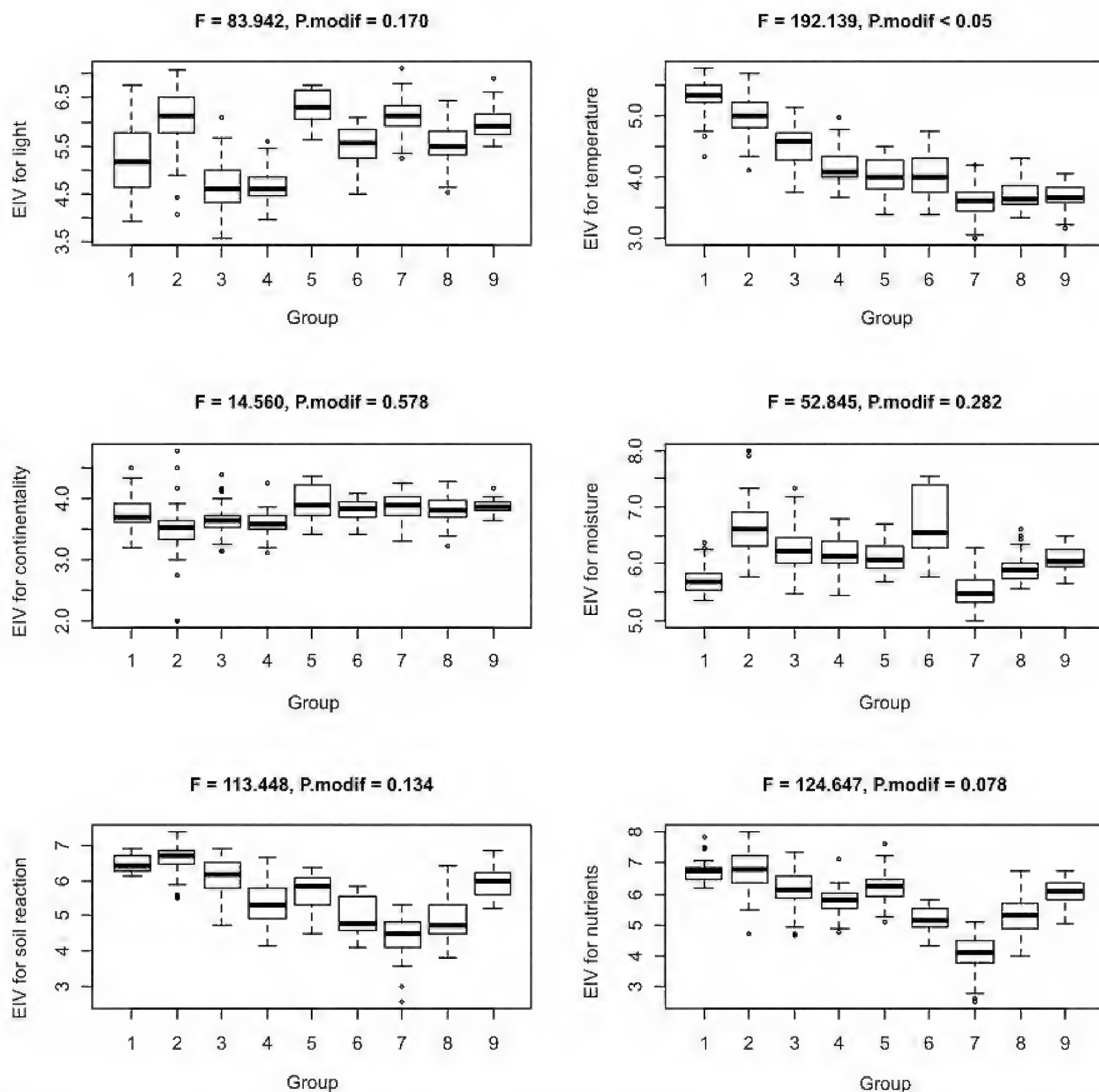


Figure 7. Summary box-and-whisker plots of mean Ellenberg indicator values (EIVs) for clusters recognized within *Mulgedio-Aconitetea* communities of the Sudetes and their foreland (SW Poland) produced by one-way permutation-ANOVA. The central line of each box indicates the median value, box boundaries the lower (25%) and upper (75%) quartiles, and whiskers the range of values. p_{modif} was calculated using a modified permutation test of significance for analysis of mean Ellenberg indicator values (EIVs), F-test statistic. Numbers of groups are the same as in Figure 2.

was 10.3%). However, the contribution of the three environmental variables (elevation, slope and the main types of bedrock) to the explained variance depended on whether we consider simple term effects or conditional effects (Table 3). Most important was elevation, but slope and bedrock type were also significant.

Discussion

Delimitation of the *Mulgedio-Aconitetea* against other classes

Separation of communities of the class *Mulgedio-Aconitetea* from other tall-herb communities of the classes

Epilobietea angustifolii Tx. et Preising ex von Rochow 1951, *Trifolio-Geranietea sanguinei* T. Müller 1962 as well as order *Filipendulo ulmariae-Lotetalia uliginosi* Passarge 1975 requires a detailed analysis of phytosociological relevés from all over Europe (or at least its central part) covering all the above-mentioned syntaxonomic units. Therefore, it significantly exceeds the scope of the presented study.

Hitherto, in synthetic studies concerning the *Mulgedio-Aconitetea* class, character species were distinguished based on *a priori* prepared lists (Michl et al. 2010) or numerical analyses (Kliment et al. 2010). For the territory of Poland, Kački et al. (2013) attempted to identify species diagnostic for the whole class as well as orders and alliances. The authors analyzed 127 relevés of tall-herb but

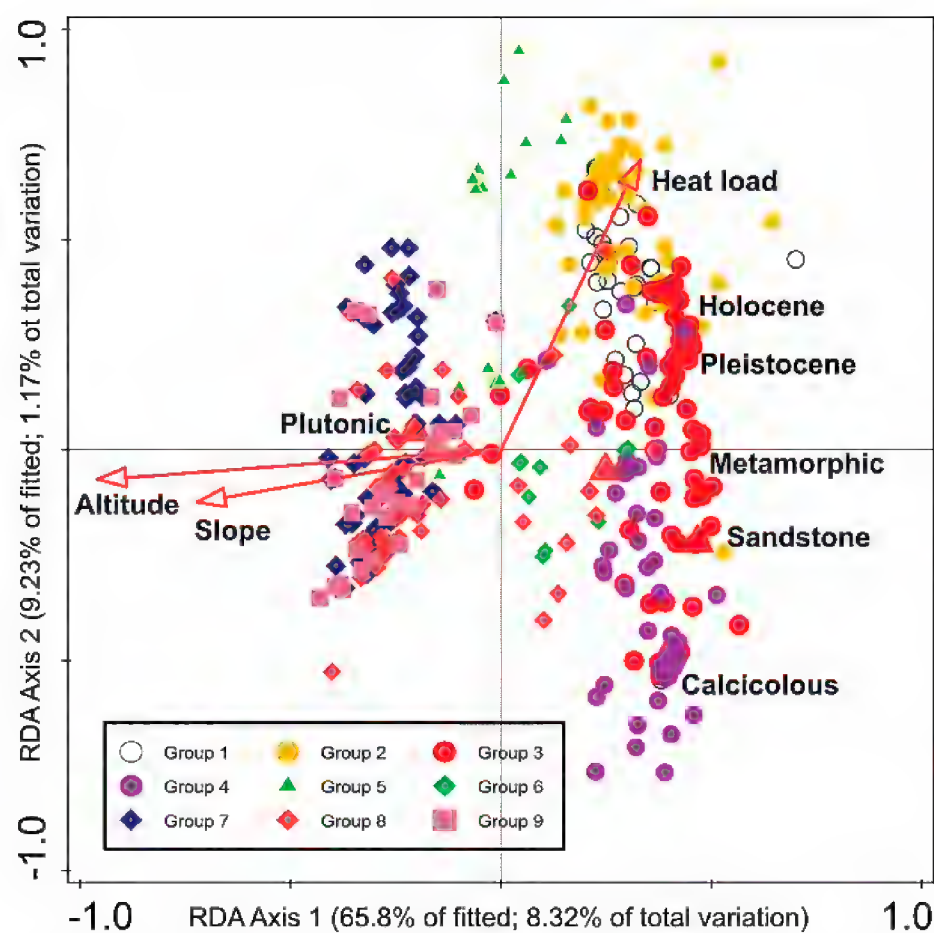


Figure 8. db-RDA plot of samples of the tall-herb communities of the Sudetes Mts. and their foothills (SW Poland) overlaid with environmental variables. Symbols indicate alliances: circles: *Petasition officinalis* (1: *Geranio phaei-Urticetum*, 2: *Petasitetum hybrydi*, 3: *Chaerophylo hirsuti-Petasitetum albi*; 4: *Prenanthesetum purpureae*); triangles: *Rumicion alpini* (5: *Rumicetum alpini*); diamonds: *Calamagrostion villosae* (6: *Poo chaixii-Deschampsietum*, 7: *Athyrietum filicis-feminae*, 8: *Crepidum conyzifoliae-Calamagrostietum*); squares: *Adenostylion alliariae* (9: *Cicerbitetum alpinae*).

Table 3. The simple term and conditional effects of analyzed environmental variables on species composition of the distinguished montane tall-herb communities, identified using db-RDA with SQRT Jaccard binary distance and Monte Carlo permutation test. Lambda - variance explained by the environmental variable [in %], *p* adj.: *p* with Bonferroni correction.

Environmental variable	Simple Term Effects			Conditional effects		
	Lambda	pseudo-F	<i>p</i> adj.	Lambda	pseudo-F	<i>p</i> adj.
Altitude	7.7	21.3	0.018	7.73	21.3	0.018
Plutonic rocks	6.7	18.3	0.018	1.06	3.0	0.018
Slope	4.7	12.4	0.018	0.77	2.2	0.018
Calcicolous rocks	2.8	7.3	0.018	0.87	2.4	0.018
Heat Load	1.8	4.6	0.018	1.00	2.8	0.018
Metamorphic rocks	1.2	3.0	0.018	0.67	1.9	0.018
Holocene deposits	2.6	6.9	0.018	0.38	1.1	> 0.05
Sandstones	0.7	1.8	0.018	0.55	1.6	> 0.05

also shrub communities accompanying watercourses. Regardless of differences in methodology, we used a similar set of diagnostic species when preparing Suppl. material 1. The *Mulgedio-Aconitetea* class is well defined by a wide range of alpine and subalpine species whose abundance increases with altitude. Therefore, at lower altitudes it may be more difficult to distinguish tall-herb phytocoenoses whose species composition refers to communities of the

classes *Epilobietea angustifolii* or *Molinio-Arrhenatheretea* Tx. 1937. However, even in such localities, species recognized as diagnostic for the *Mulgedio-Aconitetea* class, such as *Silene dioica*, *Stellaria nemorum*, *Chaerophyllum hirsutum*, *Anthriscus nitida* or *Petasites albus* regularly appear (Table 1). In this respect, an important aspect of our adopted classification system is that we included in the *Mulgedio-Aconitetea* class the order *Petasito-Chaerophylletalia*, which is in line with the concept of Kliment et al. (2010) and Mucina et al. (2016), but in contrast to Michl et al. (2010). This solution is supported by the presence of species of this class in communities belonging to this order, although their proportion gradually decreases with decreasing elevation. Moreover, these are communities associated with the valleys of montane and submontane watercourses, in contrast to other tall-herb communities of the *Epilobietea angustifolii* or *Artemisietea vulgaris* classes.

Subdivision of the *Mulgedio-Aconitetea* into orders and alliances

Despite recognition at both regional and supra-regional scales, there is still no general agreement on the syntaxonomy of tall-herb communities of the class *Mulgedio-Aconitetea*. The synthesis carried out by Michl et al. (2010) used a total of 993 relevés from all over Central and Northern Europe, and indicates the presence of a single order *Calamagrostietalia villosae* with five alliances in Central Europe: *Adenostylion alliariae*, *Rumicion alpini*, *Calamagrostion villosae*, *Calamagrostion arundinaceae* (Luquet 1926) Oberd. 1957 and *Arunco dioici-Petasition albi* Br.-Bl. et Sutter 1977). By contrast, Mucina et al. (2016) distinguished four orders with multiple alliances in Central Europe:

1. *Adenostyletalia alliariae*: Tall-herb vegetation with three Central European alliances *Adenostylion alliariae* (on siliceous substrates at high altitudes in the nemoral zone of Europe), *Dryopterido filicis-maris-Athyrium distentifolii* (Holub ex Sýkora et Štursa 1973) Jeník et al. 1980 (on fertile soils at high altitudes of the Alps, Carpathians, Hercynicum and Scandinavia), *Delphinion elati* Hadač in Hadač et al. 1969 (calcicolous tall-herb vegetation of the Carpathians).
2. *Calamagrostietalia villosae*: Tall-grass and herb-rich vegetation on nutrient-poor soils of the Alps, Carpathians and Hercynicum with three Central European alliances: *Calamagrostion villosae* (tall-herb and herb-rich vegetation on acidic soils in the subalpine and alpine belts of the Alps, Carpathians and Hercynicum), *Trisetion fusci* Krajina 1933 (on alluvial acidic soils along alpine streams of the Carpathians) and *Calamagrostion arundinaceae* (of tall-grass and herb-rich vegetation on dry acidic soils in the upper montane and subalpine belts of the mountain ranges of suboceanic Europe).
3. *Petasito-Chaerophylletalia*: Tall-herb vegetation on nutrient-rich soils along mountain streams of

Central Europe, the Balkans and the Apennines of order with two Central European alliances: *Petasition officinalis* (vegetation on raw alluvia of streams in the upper colline to supramontane belts of the Carpathians and the Hercynicum) and *Arunco dioici-Petasition albi* (in the montane and supramontane belts of the Alps).

4. *Senecioni rupestris-Rumicetalia alpini*: Tall-herb anthropogenic vegetation on nutrient-rich soils in the upper montane to alpine belts with the single alliance *Rumicion alpini*.

Here we adopted the concept of four orders of Mucina et al. (2016), because it is the only consistent proposal for a syntaxonomic classification of all plant communities in Europe at the level of classes, orders and alliances. We acknowledge that this proposal is not based on a detailed phytosociological analysis, and may change in the future. As the syntaxonomic division of the *Mulgedio-Aconitetea* class presented by Mucina et al. (2016) is complex, our discussion focuses on the alliances and orders known from Central Europe (including the Hercynicum), and omits higher units typical of Southern Europe, the Balkans and the boreal-subarctic group of orders. What distinguishes our study from those of Michl et al. (2010) and Mucina et al. (2016) is the presence of two, clearly distinctive groups of tall-herb communities. The first group includes colline-montane tall-herb communities accompanying watercourses at elevations between 200 and 1000 m a.s.l. which are rich in nemoral and nitrophilic species. We associate this group with the order *Petasito-Chaerophylletalia*, which Michl et al. (2010) do not distinguish at all. The second group consists of alpine communities that according to Michl et al. (2010) belong to one order *Calamagrostietalia villosae*, and according to Mucina et al. (2016) belong to three different orders. Some deviations of the classification proposed by us from these earlier studies are due to several facts. First, as we already mentioned, the material analyzed was strongly differentiated along the elevational gradient by inclusion of submontane tall-herb communities. Second, in the case of the *Rumicetum alpini* and *Poo chaixii-Deschampsietum cespitosae* associations, we faced the limited number of relevés, which may also affect the final classification. Therefore, it is difficult to determine which of these two above-mentioned supra-regional classifications better reflects the actual diversity of tall-herb communities in the Sudetes Mts. Nevertheless, our presented findings indicate a need for future syntheses at larger spatial extent to evaluate whether the pattern observed in the Sudetes Mts. is a local phenomenon or may contribute to changes in a general syntaxonomic scheme.

Justification and circumscription of associations

The main discrepancies occur for the communities classified here in the *Petasito-Chaerophylletalia* order (Groups 1-4). The first problems concern the assignment of the

Geranio phaei-Urticetum to the order *Petasito-Chaerophylletalia*. Phytocoenoses of this type were described for the first time by Hadač et al. (1969) from the Dolina Siedmich Prameňov (Belaer Tatras) at elevations of 1265–1310 m a.s.l. The association is also listed as quite common in the Austrian Alps and their foothills, especially on calcareous substratum (Mucina 1993), and reported from the Tatra Mts. in Poland, (Balcerkiewicz 1978). Due to floristic composition of this association, Michl et al. (2010), included it in the *Rumicion alpini*. However, their decision was based only on 6 relevés in total [2 relevés of Hadač et al. (1969) and four relevés of Kliment (1989, 1991)], missing for example the relevés published by Świerkosz et al. (2002). The latter material documents also submontane and even colline forms of the association. The data analyzed in the present study (33 relevés) show a wide altitudinal range of this community, which is not limited to the highest mountain parts (such as the *Rumicetum alpini*), but develops from the foothills to the subalpine zone, on the stream terraces covered by soils enriched with nitrogen due to high anthropogenic pressure. Altitudinal variation translates into internal variation in species composition of the association (Świerkosz et al. 2002). The phytocoenoses described by Hadač et al. (1969) and Balcerkiewicz (1978) from higher elevation in the Tatra Mts. differ from those described from the Sudetes only in the presence of three species from the class *Mulgedio-Aconitetea* (*Carduus personata*, *Rumex arifolius* and *Epilobium alpestre*). The last two species occur sporadically. On the other hand, the species composition is dominated, as in the case of forms at lower elevations, by *Urtica dioica*, *Geum urbanum*, *Rumex obtusifolius*, *Dactylis glomerata*, *Aegopodium podagraria*, *Chaerophyllum aromaticum* and *Ranunculus repens* (see Hadač et al. 1969, pp. 216–217). Nevertheless, it appears that *Geranio phaei-Urticetum* is a well-differentiated floristically and coherent unit, with a large group of its own diagnostic species. At the same time, due to the large number of nitrophilous species considered to be distinctive for the *Petasition officinalis*, and which occur also in other associations of this alliance, it seems reasonable for us to include the group 1 in the order *Petasito-Chaerophylletalia* rather than in *Senecioni rupestris-Rumicetalia alpini*. This is especially prudent since the latter aggregates tall-herb anthropogenic vegetation on nutrient-rich soils in the upper montane to alpine belts, with common occurrence of subalpine species (e.g., *Ochlopoa supina*, *Peucedanum ostruthium*, *Rumex arifolius*, *Senecio nemorensis*, *Alchemilla glabra*, *Adenostyles alliaria* and *Athyrium distentifolium*).

An additional point of debate is the placement of the *Petasitetum hybridi*. Traditionally, this association is not placed in the class *Mulgedio-Aconitetea*, but considered as a lowland community, and thus placed in tall-herb classes of the lowlands. A typical stand of the *Petasition officinalis* according to Kliment and Jarolímek (2002: p. 107) is represented by the relevé 1 on page 134 in Sillinger (1933). According to Michl et al. (2010), this type relevé should be assigned to the lowland tall-herb communities due to the prevalence of many diagnostic species of the former

Artemisietea vulgaris and *Filipendulo ulmariae-Calystegietea sepium* Géhu et Géhu-Franck 1987 (e.g., *Aegopodium podagraria*, *Anthriscus sylvestris*, *Filipendula ulmaria*, *Galium aparine*, *Petasites hybridus*). Moreover, Michl et al. (2010) suggest classifying the *Petasition officinalis* within the *Filipendulo ulmariae-Calystegietea sepium*, largely corresponding to the order *Convolvuletalia sepium* Tx. ex Moor 1958 according to Mucina et al. (2016). A similar solution is applied e.g. in Czechia where the whole alliance *Petasition hybridi* Sillinger 1933 is included in the class *Galio-Urticetea* Passarge ex Kopecký 1969 (Laníková et al. 2009), corresponding to the *Epilobietea angustifolii* in Mucina et al. (2016). In Poland, the association is included in the alliance *Aegopodion podagrariae* within the class *Artemisietea vulgaris* (Matuszkiewicz 2012), whereas Austrian and German synthesis typically place it in the order *Lamio albi-Chenopodietalia boni-henrici* Kopecký 1969 within the class *Galio-Urticetea* (Hilbig et al. 1972; Mucina 1993; Pott 1993). A contrasting approach is presented by Mucina et al. (2016) who describe the *Petasition officinalis* as „tall-herb vegetation on raw alluvia of streams in the upper colline to supramontane belts of the Carpathians and the Hercynicum” and include it in the order *Petasito-Chaerophylletalia* within the class *Mulgedio-Aconitetea*. This solution has also been supported in other regional classifications, especially in Slovakia (Kliment and Jarolímek 2002; Kliment et al. 2010). Kliment et al. 2010 (Table 1, col. 8) indicated both *Geranium phaeum* and *Petasites hybridus* as diagnostic species for the order *Petasito-Chaerophylletalia*. Similar to the studies of Jarolímek et al. (2002) and Kliment et al. (2010), in our dataset, diagnostic species for the *Mulgedio-Aconitetea* still appear in the *Petasitetum hybridi* regularly (e.g., *Petasites albus*, *Chaerophyllum hirsutum*, *Primula elatior*, *Stellaria nemorum*), or sporadically (*Silene dioica*, *Geranium sylvaticum*, *Veratrum album*, *Aconitum variegatum*, *Delphinium elatum*). There are clear connections among these species, through the presence of low-mountain and nitrophilous species to the communities of the classes *Epilobietea angustifolii* and *Molinio-Arrhenatheretea*, particularly to the alliance *Filipendulo-Petasition* Br.-Bl. ex Duvigneaud 1949. However, this reference is also found in Table 1 col. 8 in Kliment et al. (2010), which presents the similar set of species as we see in our data (e.g., *Chaerophyllum aromaticum*, *Aegopodium podagraria*, *Filipendula ulmaria*, *Rumex obtusifolius*, *Lamium maculatum*, *Cirsium oleraceum*, *Galium aparine*, *Lysimachia nummularia*, *Schedonorus giganteus* and others). It should also be noted that the latest study on the differentiation of the class *Molinio-Arrhenatheretea* in Poland (Kącki et al. 2021) does not list herbaceous communities with *Petasites hybridus* within this class at all.

The next two associations that we distinguished (*Chaerophyllo hirsuti-Petasitetum albi* and *Prenanthesetum purpureae*) overlap with the range of the broadly defined *Chaerophyllo hirsuti-Cicerbitetum alpinae*. However, in our opinion, differences in species composition and

ecological characteristics fully justify their separation. The association *Chaerophyllo hirsuti-Petasitetum albi* is the central unit of the alliance, because of the large amplitude of the occupied habitat types, wide altitudinal range, and the species composition, determined by the dominance of *Petasites albus*, which is common in the Sudetes Mts., as well as the constant presence of species of the *Carpi-no-Fagetea* class. Since the *Petasitetum albi* is recognized as *nomen ambiguum* (Kočí 2001, 2007) we propose to restore the name *Chaerophyllo hirsuti-Petasitetum albi*, because it almost perfectly fits the species combination (most of the species occurring in the type relevé (Sýkora and Hadač 1984) occurred also in the Table 1, col. 3) and ecological characteristics (Hadač and Soldán 1989). Despite that, some authors included this association in the mire vegetation of the class *Montio-Cardaminetea* Br.-Bl. et Tx. ex Klika et Hadač 1944 (Hrivnák et al. 2005), which is not consistent with our knowledge about phytocoenoses discussed here. They are usually present in valleys of streams flowing through deciduous forests, hence the randomized EIVs for nutrients and soil reaction calculated for this association are clearly higher than that for the *Prenanthesetum purpureae*. The latter is similar in terms of habitat but present in acidophilous beech forests (especially *Calamagrostio villosae-Fagetum* Mikyška 1972 and *Calamagrostio arundinaceae-Fagetum* Sýkora 1971) and in artificial spruce forests replacing them. Moreover, it is also marked by lower EIVs for temperature, which are connected to the higher elevations the association occupies in relation to the *Chaerophyllo hirsuti-Petasitetum albi*. Therefore, we think that the separation of these two associations is fully justified as in their original description (Sýkora and Hadač 1984). The species composition of the *Prenanthesetum purpureae* corresponds to the original diagnosis of Bolleter (1921, p. 86, relevés 4 and 5), although several Alpine species (e.g., *Aconitum lycoctonum*, *Ranunculus aconitifolius* or *Crepis pyrenaica*) are absent from the Sudetes Mts.

We propose to include both these associations in the order *Petasito-Chaerophylletalia* and in the alliance *Petasition officinalis*, instead of in the *Calamagrostietalia villosae* and the alliance *Arunco dioici-Petasition albi*, as proposed by Michl et al. (2010). We decided on the first option based on the concept of Mucina et al. (2016), who consider the alliance *Arunco-Petasition albi* as restricted to the Alps, while the *Petasition officinalis* alliance includes tall-herb vegetation on raw alluvia of streams in the upper colline to supramontane belts of the Carpathians and the Hercynicum. Many differential species of this alliance occurred in both associations (Table 1), whereas species from subalpine alliances (*Calamagrostion villosae*, *Adenostylion alliariae*) were scarce.

Group 5 embraces montane, nitrophilous phytocoenoses with a dominance of *Rumex alpinus* and corresponds to the *Rumicetum alpini*, an association regularly mentioned both in regional studies (Karner and Mucina 1993; Kočí 2001, 2007; Stachurska-Swakoń 2008; Matuszkiewicz 2012) and the supraregional synthesis by Michl et

al. (2010). However, Stachurska-Swakoń (2009) split the Carpathian communities with *Rumex alpinus* between two classes. She distinguished two associations (*Aconito firmit-Rumicetum alpini* Unar in Unar et al. 1985 and *Heracleo palmati-Rumicetum alpini* Oltean et Dihoru 1986) with natural character and included them in the class *Mulgedio-Aconitetea*, while placing the montane synanthropic association *Rumicetum alpini* in the *Galio-Urticetea* class. The diversity of these tall-herb phytocoenoses in the Sudetes Mts. is not as high as in the Carpathians and clearly corresponds to *Rumicetum alpini*. However, similar to Michl et al. (2010), we treat the latter, as belonging to the alliance *Rumicion alpini* within the *Mulgedio-Aconitetea* class.

Group 6 includes relevés of mountain tall-grass communities that most often accompany local wetlands, spring zones and stream valleys in open areas. Kočí (2001, 2007) includes them in the *Violo sudeticae-Deschampsietum cespitosae* (Jeník et al. 1980) Kočí 2001, an association considered endemic to the Eastern Sudetes, which has been synonymized with the *Poo chaixii-Deschampsietum cespitosae* in the supra-regional study of Michl et al. (2010).

Group 7 represents alpine tall-grass stands in the Karkonosze Mts. The analyzed data was mainly obtained from the literature (Matuszkiewicz and Matuszkiewicz 1974). Fabiszewski and Wojtuń (2001) documented a substantial decrease in the mean number of species per plot from 21.8 to 13.7 in comparison to data collected in the 1970s. This decline was reflected by a complete loss of species such as *Aconitum plicatum*, *Lactuca alpina*, *Geum montanum*, *Hieracium alpinum*, *Hypericum maculatum*, *Potentilla aurea* and a significant decrease in abundance of *Adenostyles alliariae*, *Huperzia selago*, *Pulsatilla alba* and *Ranunculus platanifolius*. Similarly, Dunajski et al. (2016) reported a 28% decrease in the total number of species within 10 permanent plots. This indicates a significant impoverishment of the composition of the tall-grass phytocoenoses in the Karkonosze Mts., which are probably caused by excessive depositions of atmospheric nitrogen (1138 mg/m²/year), favouring the expansion of graminoids, especially *Calamagrostis villosa* and *Avenella flexuosa* (Fabiszewski and Wojtuń 2002). In the numerical analysis, the previously described association *Bupleuro-Calamagrostietum arundinaceae* is not distinguishable and is a part of the cluster of the *Crepido-Calamagrostietum*. In recent years, phytocoenoses whose species composition relates to the former association have not been examined. Therefore, both its presence in the Karkonosze Mts. and distinctness from the *Crepido-Calamagrostietum* require further research.

Group 8 embraces stands with *Athyrium distentifolium* and specific combination of acidophytes of the alliance *Calamagrostion villosae* and species of the *Adenostylion alliariae*. Following Michl et al. (2010) and due to high abundance of graminoids (*Calamagrostis villosa*, *C. arundinacea*, *Avenella flexuosa*, *Luzula luzuloides*) and acidophilous ferns (*Dryopteris dilatata*, *D. carthusiana*, *Gymnocarpium dryopteris*, *Phegopteris connectilis*) (compare Karner and Mucina 1993), we included this group in the

alliance *Calamagrostion villosae*. The species composition of the phytocoenoses corresponds well to the association *Athyrietum filicis-feminae* distinguished by Höfler and Wendelberger (1960), and more precisely to its variant with *Thalictrum aquilegifolium* (Höfler and Wendelberger 1960, pp. 141–142, relevés 3–5). In the latter, *Athyrium distentifolium* is mainly accompanied by *Calamagrostis villosa*, *Oxalis acetosella*, *Stellaria nemorum*, *Rumex arifolius*, *Veratrum album*, *Viola biflora*, *Rubus idaeus* and *Urtica dioica*, and sporadically also by *Athyrium filix-femina*. Michl et al. (2010) recognized the primacy of the above name over later ones, while the lectotypus was designated by Karner and Mucina (1993).

Group 9 includes relevés from the highest parts of the Karkonosze Mts. We classified the communities from this group to the *Cicerbitetum alpinae* (within the *Adenostylion alliariae* alliance), which was also reported by Michl et al. (2010) from the Sudetes Mts. The species composition of vegetation plots reported from the Karkonosze Mts. corresponds well to the original diagnosis of Bolleter (1921, Table p. 86, relevés 6–7) with occurrence of *Adenostyles alliariae*, *Lactuca alpina*, *Rumex arifolius*, *Geranium sylvaticum*, *Chaerophyllum hirsutum*, *Dryopteris filix-mas*, *Viola biflora*, *Silene dioica* and others. However, similar to the *Prenanthesetum purpureae*, some Alpine species do not occur here. Therefore, distinguishing the separate associations such as *Adenostyletum alliariae*, *Aconitetum firmit* and *Petasitetum kablikiani* (compare Matuszkiewicz 2012) does not seem to be justified.

It should be noted that we had no data of the *Arunco-Doronicetum austriaci* from our study region (neither own records, nor literature data), which has been reported from other parts of the Sudetes Mts. (Matuszkiewicz 2012). Most of the phytocoenoses with the dominance of *Aruncus sylvestris* belong to the *Arunco vulgaris-Lunarietum redivivae* Sádlo et Petřík in Chytrý 2009, which are synanthropic in the Polish part of the Sudetes Mts., and not directly connected to watercourses. They usually occupy places under gaps in the canopy (e.g., in rich beech forests), forest clearings, or unforested steep slopes, where they form one of the successional stages (in Świerkosz and Reczyńska 2016 as comm. *Polygonatum verticillatum-Ranunculus platanifolius*; mentioned also in Kaćki et al. 2019).

Conclusions

In this comprehensive regional typology of the *Mulgedio-Aconitetea* in the Polish Sudetes Mts. we distinguished nine associations with relatively clear floristic and ecological separation. For convenience, we largely adopted the higher syntaxa of the current EuroVegChecklist (Mucina et al. 2016), thus, accepting four orders with one alliance each. It should be noted that this “conservative” approach contrasts to our ordination diagram and partly also our vegetation table, according to which there are rather two main groups, namely colline-montane and alpine

communities. This differs from the four groups as found in Mucina et al. (2016), and the one as in Michl et al. (2010). The first group embraces phytocoenoses accompanying watercourses of elevations between 200 and 1000 m a.s.l. and with high proportion of species such as *Petasites albus*, *P. hybridus*, *Geranium phaeum*, *Prenanthes purpurea*, *Aegopodium podagraria*, *Urtica dioica* and, depending on local conditions, also numerous species typical of forests or meadows. The second group includes alpine communities, most often developing above the upper forest zone (1100–1470 m a.s.l., exceptionally lower), in which alpine species dominate, such as *Athyrium distentifolium*, *Aconitum plicatum*, *Adenostyles alliariae*, *Ranunculus platanifolius*, *Lactuca alpina*, *Rumex alpinus* or *Senecio nemorensis*. These groupings may suggest that the division of alpine communities into three independent orders as adopted by Mucina et al. (2016) will not be confirmed during the analysis of a broader phytosociological material. It will be the task for future syntheses at larger spatial extents to evaluate whether this pattern is a Sudetian idiosyncrasy, or more widespread, and should thus be reflected in a general syntaxonomic scheme.

References

- Anioł-Kwiatkowska J, Malicki M (2005) *Rumex alpinus* L. in Karkonosze (the Sudeten Mountains) apophyte or anthropophyte? Proceedings of the 8th International Conference on Ecology and Management of Alien Plant Invasions 5–12.09.2005, Katowice, Poland.
- Balcerkiewicz S (1978) Vegetation of Polana Chochołowska (Chochołowska Clearing) in the West Tatras. In: Wojterski TW (Ed.) Guide to the Polish International Excursion 1–20 June 1978. Uniwersytet im. Adama Mickiewicza w Poznaniu. Serie Biologia 11: 355–381.
- Berg C, Welk E, Jager EJ (2017) Revising Ellenberg's indicator values for continentality based on global vascular plant species distribution. *Applied Vegetation Science* 20: 482–493. <https://doi.org/10.1111/avsc.12306>
- Blachowski J, Markowicz-Judycka E, Zięba D [Eds] (2005) Opracowanie ekofizjograficzne dla województwa dolnośląskiego [Eco-physiographic study for the Lower Silesian Voivodship]. Wojewódzkie Biuro Urbanistyczne we Wrocławiu, Wrocław, PL, 268 pp. [in Polish]
- Bolewski A, Parachoniak W (1988) Petrografia [Petrography]. Wydawnictwo Geologiczne, Warszawa, PL, 656 pp. [in Polish]
- Bolleter R (1921) Vegetationsstudien aus dem Weisstannental. *Jahrbuch der St. Gallischen Naturwissenschaftlichen Gesellschaft* 57: 1–140.
- Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science* 13: 79–90. <https://doi.org/10.1111/j.1654-1103.2002.tb02025.x>
- Dengler J, Berg C, Jansen F (2005) New ideas for modern phytosociological monographs. *Annali di Botanica Nuova Serie* 5: 193–210.
- Dunajski A, Szymura TH, Szymura M (2016) Recent high mountain vegetation structure in the Karkonosze Mts. – results from the system of permanent plots. *Fragmenta Floristica et Geobotanica Polonica* 23: 57–72.
- Ellenberg H, Weber HE, Düll R, Wirth W, Werner W, Paulißen D (1991) Zeigerwerte von Pflanzen in Mitteleuropa. 1 Auflage, Scripta Geobotanica 18: 1–258.
- Euro+Med (2006-) The Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity. <http://ww2.bgbm.org/EuroPlusMed/> [accessed 2 Dec 2020]
- Fabiszewski J, Wojtuń B (2001) Contemporary floristic changes in the Karkonosze Mts. *Acta Societatis Botanicorum Poloniae* 70: 237–245. <https://doi.org/10.5586/asbp.2001.031>
- Fischer HS (2015) On the combination of species cover values from different vegetation layers. *Applied Vegetation Science* 18: 169–170. <https://doi.org/10.1111/avsc.12130>
- Gleason J (2013) Comparative power of the Anova, randomization Anova, and Kruskal-Wallis Test. Ph.D. thesis, Wayne State University Dissertations 658, Detroit, MI, US. https://digitalcommons.wayne.edu/oa_dissertations/658
- Hadač E, Březina P, Ježek V, Kubička J, Hadačová V, Vondráček M (1969) Die Pflanzengesellschaften des Tales “Dolina Siedmich prameňov” in der Belaer Tatra. Vydavateľstvo Slovenskej Akadémie Vied, Bratislava, SK, 343 pp.
- Hadač E, Soldán Z (1989) Rostlinná společenstva pramenišť a horských potokd v Bukovských vrších na severovýchodním Slovensku [Plant communities of springs and mountain brooks in the Bukovské vrchy hills, NE Slovakia]. *Preslia* 61: 343–353.
- Hennekens SM, Schaminée JHJ (2001) TURBOVEG, a comprehensive data base management system for vegetation data. *Journal of Vegetation Science* 12: 589–591. <https://doi.org/10.2307/3237010>
- Hilbig W, Heinrich W, Niemann E (1972) Übersicht über die Pflanzengesellschaften des südlichen Teiles der DDR IV. Die nitrophilen Saumgesellschaften. *Hercynia N. F.* 9: 229–270.
- Höfler K, Wendelberger G (1960) Botanische Exkursion nach dem “Märchenwald” im Amertal (Hohe Tauern). *Verhandlungen der Zoologisch-Botanischen Gesellschaft Wien* 100: 112–145.
- Hrivnák R, Kochjarová J, Blanár D, Šoltés D, Mišíková K (2005) Vegetácia pramenísk triedy *Montio-Cardaminetea* na Muránskej planine

Data availability

All analyzed relevés (including environmental variables) are available on request through the VESTA Database (Global Index of Vegetation-Plot Databases, ID: EU-PL-004) and the Polish Vegetation Database (Global Index of Vegetation-Plot Databases, ID: EU-PL-001).

Author contributions

K.Ś. and K.R. planned the research, K.Ś. and K.R. conducted the field sampling, K.Ś. performed the statistical analyses and led the writing, while both authors critically revised the manuscript.

Acknowledgments

We are grateful to Jürgen Dengler, Kiril Vassilev and two anonymous Reviewers for their valuable comments on the manuscript.

- [Water-spring vegetation of the class *Montio-Cardaminetea* in the Muránska planina Mts.]. *Reussia* 2: 153–172.
- Jarolímek I, Kliment J, Valachovič M (2002) The syntaxonomical revision of the riparian plant communities dominated by *Petasites hybridus* in Slovakia. *Biologia* 57: 471–492.
- Jarolímek I, Šibík J, Hegedúšová K, Janišová M, Kliment J, Kučera P, Májeková J, Michálková D, Sadloňová J, ... Zaliberová M (2008) A list of vegetation units of Slovakia. In: Jarolímek I, Šibík J (Eds) Diagnostic, constant and dominant species of the higher vegetation units of Slovakia. Veda, Bratislava, SK, 295–329.
- Jupke JF, Schäfer RB (2020) Should ecologists prefer model- over distance-based multivariate methods? *Ecology and Evolution* 10: 2417–2435. <https://doi.org/10.1002/ece3.6059>
- Karner P, Mucina L (1993) *Mulgedio-Aconitetea*. In: Grabherr G, Mucina L (Eds) Die Pflanzengesellschaften Österreichs. Teil II. Natürliche waldfreie Vegetation. Gustav Fischer Verlag, Jena, DE, 468–505.
- Kącki Z, Śliwiński M (2012) The Polish Vegetation Database: Structure, resources and development. *Acta Societatis Botanicorum Poloniae*, 81: 75–79. <https://doi.org/10.5586/asbp.2012.014>
- Kącki Z, Czarniecka M, Swacha G (2013) Statistical determination of diagnostic, constant and dominant species of the higher vegetation units of Poland. *Monographiae Botanicae* 103: 1–267. <https://doi.org/10.5586/mb.2013.001>
- Kącki Z, Szymura M, Świerkosz K, Swacha G, Pender K (2018) Zbiorowiska roślinne Gór Stołowych [Plant communities of the Stołowe Mts.] In: Kabała C (Ed.) Góry Stołowe – przyroda i ludzie [The Stołowe Mts. – Nature and people]. Park Narodowy Gór Stołowych, Kudowa Zdrój, 311–328.
- Kącki Z, Swacha G, Lengyel A, Korzeniak K (2020) Formalized hierarchically nested expert system for classification of mesic and wet grasslands in Poland. *Acta Societatis Botanicorum Poloniae* 89: 8941. <https://doi.org/10.5586/asbp.8941>
- Kliment J (1989) *Carduetum personatae* Hadač et al. 1969 vo Vel'kej Fatre [*Carduetum personatae* Hadač et al. 1969 in the Vel'ká Fatra Mts.]. *Biológia* 44: 451–457.
- Kliment J (1991) *Geranio phaei-Urticetum dioicae* Hadač et al. 1969 vo Vel'kej Fatre [*Geranio phaei-Urticetum dioicae* Hadač et al. 1969 in the Vel'ká Fatra Mts.]. *Biológia* 46: 419–425.
- Kliment J, Jarolímek I (2002) Syntaxonomical revision of the *Petasites kablikianus* communities (*Petasition officinalis*) in the West Carpathians. *Biológia* 57: 101–118.
- Kliment J, Jarolímek I, Šibík J, Valachovič M (2004) Syntaxonomy and nomenclature of the communities of the orders *Calamagrostietalia villosae* and *Adenostyletalia* in Slovakia. *Thaiszia* 14: 93–15.
- Kliment J, Šibík J, Šibíková I, Jarolímek I, Dúbravcová Z, Uhlířová K (2010) High-altitude vegetation of the Western Carpathians - a syntaxonomical review. *Biologia* 65: 965–989. <https://doi.org/10.2478/s11756-010-0109-4>
- Kočí M (2001) Subalpine tall-forb vegetation (*Mulgedio-Aconitetea*) in the Czech Republic: syntaxonomical revision. *Preslia* 73: 289–331.
- Kočí M (2007) Subalpínská vysokobylinná a křovinná vegetace (*Mulgedio-Aconitetea*). Subalpine tall-forb and deciduous-shrub vegetation. In: Chytrý M (Ed.) Vegetace České republiky. 1. Travinná a keříčková vegetace [Vegetation of the Czech Republic. 1. Grassland and Heathland Vegetation]. Academia, Praha, CZ, 92–131.
- Kočí M, Chytrý M, Tichý L (2003) Formalized reproduction of an expert-based phytosociological classification: A case study of subalpine tall-forb vegetation. *Journal of Vegetation Science* 14: 601–610. <https://doi.org/10.1111/j.1654-1103.2003.tb02187.x>
- Láníková D, Kočí M, Sádlo J, Šumberová K, Hájková P, Hájek M, Petřík P (2009) Nitrofilní vytrvalá vegetace vlhkých a mezických stanovišť (*Galio-Urticetea*). Nitrophilous perennial vegetation of wet to mesic habitats. In: Chytrý M (Ed.) Vegetace České republiky. 2. Ruderální, plevelová, skalní a suťová vegetace [Vegetation of the Czech Republic 2. Ruderal, weed, rock and scree vegetation]. Academia, Praha, CZ, 290–378.
- Macko S (1950) Zespoły roślinne w Karkonoszach. Część I. Karkonosze wschodnie [Plant communities in the Karkonosze Mts. Part I. Eastern Karkonosze]. *Acta Societatis Botanicorum Poloniae* 21: 591–683. [in Polish] <https://doi.org/10.5586/asbp.1952.036>
- Matuszkiewicz W (2012) Przewodnik do oznaczania zbiorowisk roślinnych Polski [A guide to the identification of plant communities of Poland]. Państwowe Wydawnictwo Naukowe, Warszawa, PL, 536 pp. [in Polish]
- Matuszkiewicz W, Matuszkiewicz A (1974) Mapa zbiorowisk roślinnych Karkonoskiego Parku Narodowego [Map of the plant communities of the Karkonoski National Park]. *Ochrona Przyrody* 40: 45–109. [in Polish]
- McCune B, Keon D (2002) Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science* 13: 603–606. <https://doi.org/10.1111/j.1654-1103.2002.tb02087.x>
- Michl T, Dengler J, Huck S (2010) Montane-subalpine tall-herb vegetation (*Mulgedio-Aconitetea*) in central Europe: large-scale synthesis and comparison with northern Europe. *Phytocoenologia* 40: 117–154. <https://doi.org/10.1127/0340-269X/2010/0040-0377>
- Mucina L (1993) *Galio-Urticetea*. In: Mucina L, Grabherr G, Ellmauer T (Eds) Die Pflanzengesellschaften Österreichs. Teil I. Anthropogene Vegetation. Gustav Fischer Verlag, Jena, DE, 203–251.
- Mucina L, Bültmann H, Dierßen K, Theurillat JP, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, ... Tichý L (2016) Vegetation of Europe: Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science* 19(Suppl. 1): 3–264. <https://doi.org/10.1111/avsc.12257>
- Mueller-Dombois D, Ellenberg H (2002) Aims and Methods of Vegetation Ecology, Reprint. The Blackburn Press, Caldwell, NJ, US, 547 pp.
- Pawłowski B, Walas J (1949) Les associations des plantes vasculaires des Monts de Czywczyn. *Bulletin International de l'Académie Polonaise des Sciences et des Lettres. Série B: Sciences Naturelles* 1: 1–181.
- Pott R (1995) Die Pflanzengesellschaften Deutschlands. 2nd ed. Verlag Eugen Ulmer, DE, 623 pp.
- R Development Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, AT. <http://www.R-project.org> [accessed 19 Dec 2021]
- Roleček J, Tichý L, Zelený D, Chytrý M (2009) Modified TWINSpan classification in which the hierarchy respects cluster heterogeneity. *Journal of Vegetation Science* 20: 596–602. <https://doi.org/10.1111/j.1654-1103.2009.01062.x>
- Šibíková I, Šibík J, Jarolímek I (2008) The tall-herb and tall-grass plant communities of the class *Mulgedio-Aconitetea* in the subalpine belt of the Krivánska Malá Fatra Mts. (Slovakia). *Hacquetia* 7: 141–159. <https://doi.org/10.2478/v10028-008-0008-1>
- Sillinger P (1933) Monografická studie o vegetaci Nízkých Tater [Monographical study of the vegetation of the Nízké Tatry]. Knižovna Sboru Výzkum Slovenska Podkarpatské Rusi Při Slovanském Ústavu Praze 6. Research Board for Slovakia and Ruthenia of the Slav Institute of Prague, Prague, CZ, 338 pp.

- Stachurska-Swakoń A (2008) Synanthropical communities with *Rumex alpinus* in the Tatra National Park (West-Carpathian). In: Kočárek P, Plášek V, Malachová K, Cimalová Š (Eds) Environmental changes and biological assessment IV. Scripta Facultatis Rerum Naturalium Universitatis Ostraviensis 186: 321–330.
- Stachurska-Swakoń A (2009) Syntaxonomical revision of the communities with *Rumex alpinus* L. in the Carpathians. Phytocoenologia 39: 217–234. <https://doi.org/10.1127/0340-269X/2009/0039-0217>
- Sýkora T, Hadač E (1984) Příspěvek k fytogeografii Adršpašsko-Teplických skal [Contribution to the phytogeography of the Adršpach-Teplice Rocks]. Preslia 56: 359–376.
- Świerkosz K, Dajdok Z, Szczęśniak E (2002) The association *Geranio phaei-Urticetum dioicae* in Southwest Poland. Polish Botanical Journal 47: 53–66.
- Świerkosz K, Reczyńska K (2013) Hygrophilous tall herb communities in the Stołowe Mts., against their diversity in the Sudetes (Poland). In: Migoń P, Kasprzak M (Eds) Sandstone Landscapes. Diversity, Ecology and Conservation. Instytut Geografii i Rozwoju Regionalnego Uniwersytetu Wrocławskiego, Wrocław, PL, 177–182.
- Świerkosz K, Reczyńska K (2016) Wstępne badania nad zróżnicowaniem zbiorowisk ziołoroślowych na terenie Śnieżnika Kłodzkiego, Gór Bystrzyckich i Orlickich (Sudety, Polska) [Preliminary research on the diversity of tall-herb communities of the Śnieżnik Kłodzki Massif, Bystrzyckie Mts., and Orlickie Mts. (Sudetes, Poland)]. Przyroda Sudetów 19: 61–74. [in Polish]
- Ter Braak CJF, Smilauer P (2012) Canoco reference manual and user's guide: software for ordination, version 5.0. Microcomputer Power, Ithaca, US, 496 pp.
- Theurillat JP, Willner W, Fernández-González F, Bültmann H, Carni A, Gigante D, Mucina L, Weber H (2021) International Code of Phytosociological Nomenclature. 4th ed. Applied Vegetation Science 24: e12491. <https://doi.org/10.1111/avsc.12491>
- Tichý L (2002) JUICE, software for vegetation classification. Journal of Vegetation Science 13: 451–453. <https://doi.org/10.1111/j.1654-1103.2002.tb02069.x>
- Tichý L, Chytrý M (2006) Statistical determination of diagnostic species for site groups of unequal size. Journal of Vegetation Science 17: 809–818. <https://doi.org/10.1111/j.1654-1103.2006.tb02504.x>
- Tichý L, Holt J (2006) Juice program for management, analysis and classification of ecological data. 1st ed. Masaryk University, Brno, CZ, 98 pp.
- Uziębło AK (2004) Subalpine populations of *Petasites kablikianus* Tausch ex. Bercht. in the Babia Góra and in the Karkonosze National Parks. In: Štursa J, Mazurski KR, Pałucki A, Potocka J (Eds) Geoekologicke problémy Krkonoše [Geo-ecological problems of the Karkonosze Mts.]. Sborník příspěvků z mezinárodní conference, November 2003, Szklarska Poręba. Opera Corcontica 41: 135–141.
- Willner W, Tichý L, Chytrý M (2009) Effects of different fidelity measures and contexts on the determination of diagnostic species. Journal of Vegetation Science 20: 130–137. <https://doi.org/10.1111/j.1654-1103.2009.05390.x>
- Zelený D, Schaffers AP (2012) Too good to be true: pitfalls of using mean Ellenberg indicator values in vegetation analyses. Journal of Vegetation Science 23: 419–431. <https://doi.org/10.1111/j.1654-1103.2011.01366.x>
- Zlatník A (1928) Aperçu de la végétation des Krkonoše (Riesengebirge). Preslia 7: 94–152.

E-mail and ORCID

Krzysztof Świerkosz (krzysztof.swierkosz@uwr.edu.pl), ORCID: <https://orcid.org/0000-0002-5145-178X>

Kamila Reczyńska (Corresponding author, kamila.reczynska@uwr.edu.pl), ORCID: <https://orcid.org/0000-0002-0938-8430>

Supplementary material

Supplementary material 1

List of species distinguishing communities of the class *Mulgedio-Aconitetea* from other non-forest communities based on literature sources

Link: <https://doi.org/10.3897/VCS.70200.suppl1>

Supplementary material 2

A detailed description of the TWINSpan analysis used to distinguish the associations described in the present paper

Link: <https://doi.org/10.3897/VCS.70200.suppl2>

Supplementary material 3

Full, sorted relevé table of the studied tall-herb communities in the Sudetes Mts. (SW Poland)

Link: <https://doi.org/10.3897/VCS.70200.suppl3>